

PREDATION AND COMMUNITY ON A COMPLEX SURFACE:
TOWARD A FRACTAL ECOLOGY

By

ROBERT GLEN LOWEN

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2001

This dissertation is dedicated to the memory of Dr. William L. Peters

ACKNOWLEDGMENTS

I wish to gratefully acknowledge the help and leadership of my major professor and committee chair Dr. Dale H. Habeck. I also wish to thank Dr. Gary R. Buckingham who has been a co-chairman in fact if not in name. This work could not have been done without the financial and logistical support of these two. I wish to thank the other members of my committee, Dr. Frank Slansky Jr. for sticking with me throughout, and Dr. Benjamin M. Bolker and Dr. Charles E. Cichra for filling in when I needed them. I also wish to thank Drs. Jon C. Allen, and C.S. "Buzz" Holling who encouraged me to think in nonlinear terms.

I extend special thanks to Dr. John R. Strayer and the late Dr. W.L. "Bill" Peters, without either of whom I would not have come to the University of Florida. I wish to thank Dr. Jerry F. Butler and all the people in his lab for providing the mosquito larvae, with special thanks to Diana Simon and Karen McKenzie. I wish to thank Dr. James Cuda and his assistant Judy Gillmore who provided laboratory space and logistic support. I also wish to thank the numerous lab assistants who helped in ways both small and large.

I wish to acknowledge the assistance of Myrna Litchfield and Debbie Hall who kept me straight when it came to University paperwork. Jane C. Medley aided the production of images used in the survey. Steve Lasley provided computer support at all levels. I thank the rest of the students and staff of the Department of Entomology and Nematology; the Division of Plant Industry; and the Center for Aquatic and Invasive Plants.

I wish to thank my parents for moral and financial support and for always encouraging me to achieve more. Above all else I wish to thank my wife Catherine for her love, support and boundless patience. Finally I wish to thank my stepchildren Erin and Bryan Brooks without whom this would have been a far less interesting ride.

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGEMENTS.....	iii
ABSTRACT.....	viii
CHAPTERS	
1 INTRODUCTION	1
2 REVIEW: COMPLEXITY AND COMMUNITY	6
Arena.....	7
Infinite Coastline.....	7
Mathematics of Noise	9
Euclidean World and its Monsters.....	11
Power Laws and a Multitude of Dimensions.....	16
Measure of the Monsters.....	18
Measure of Nature	21
Fractal Geometry of Nature	24
Animal Community	26
Passive Physical Response.....	26
Behavioral Response.....	28
Trophic/Energetic Response	29
Competition Response	32
Succession in Time or Space	35
Summary.....	38
3 PERCEPTION OF COMPLEX SURFACES	40
Rules for Box-Counting.....	40
Apparent Dimension.....	41
Minimum Size of Existence.....	43
All Things are Relative	45
Rule of Averaging.....	49
Testing Real-World Validity	53
Introduction.....	54
Materials and Methods.....	54
Results.....	61
Discussion	69
Conclusions.....	70

4	REVIEW: COMPLEXITY AND COMMUNITY	73
	Prelude to the Three-Point Interaction	73
	Predator-Prey Interactions	73
	Parts of Predation	73
	Functional Response	75
	Optimal Foraging	77
	Prey Size Affected by Predation Technique	82
	Impact of Arena on Predator-Prey Interactions	84
	Behavioral Effects	87
	Mechanistic Effects	90
	Changes in density	90
	Changes in form	96
	Summary	102
5	PREDATION ON A COMPLEX SURFACE	105
	Predicting the Obvious	113
	Introduction	113
	Materials and Methods	115
	Results	117
	Discussion	119
	Predator Size in a Complex Environment	120
	Introduction	120
	Materials and Methods	121
	Results	122
	Discussion	125
	Prey Size in a Complex Environment	135
	Introduction	135
	Materials and Methods	136
	Results	137
	Discussion	141
	Conclusions	151
6	REVIEW: PREDATION AND COMMUNITY	155
	How Do You Measure Community Shape?	156
	Richness and Diversity	157
	Size Versus Frequency	159
	Clumps	165
	Predator Effect on Community Shape	169
	Direct Effects	170
	Cascade Effects	177
	Predation as a Constant Force	180
	Arena Effect on Community Shape	188
	Amount of Structure	189
	Variety of Structure	192
	Form of Structure	195
	Summary	205

7	COMMUNITY ON A COMPLEX SURFACE.....	211
	Effect of Plant Species on Community Shape	212
	Materials and Methods.....	212
	Results.....	215
	Discussion	237
	Effect of Plant Form on Community Shape.....	240
	Materials and Methods.....	240
	Results.....	241
	Discussion	264
	Conclusions.....	270
8	SUMMARY AND CONCLUSIONS	276
	Measurement of Form.....	277
	Form as an Interactive Surface	281
	Form as a Community Template	291
	Alternative Explanations.....	307
	Future Research	316
	APPENDIX MATLAB LANGUAGE COMPUTER PROGRAMS	319
	REFERENCES	321
	BIOGRAPHICAL SKETCH	348

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

PREDATION AND COMMUNITY ON A COMPLEX SURFACE:
TOWARD A FRACTAL ECOLOGY

By

Robert Glen Lowen

August 2001

Chairman: Dale H. Habeck

Major Department: Entomology and Nematology

The technique of box-counting as a method for measuring fractal dimensions is reviewed. A set of three axioms are developed that standardize methods and allow for multi-scale evaluation of complexity. A program was written that performed box-counting on images of aquatic plants. Results were highly correlated with mean subjective evaluation of complexity. Box-counting plots of plant images were used to determine indices of prey detectability and accessibility. Detectability was defined as being proportional to the mean prey size over the mean size of plant surface at the scale of the prey. Accessibility was defined as being proportional to the mean size of plant surface at the scale of the predator over the mean size of plant surface at the scale of the prey. Laboratory experiments of fish predation on mosquito larvae were found to be highly correlated to both indices.

Field samples of aquatic arthropods were taken from single species patches of *Myriophyllum spicatum* L., *Hydrilla verticillata* (L.f.), and *Vallisneria americana* Michx. Bundles of plastic aquarium plants resembling each of these species were placed at all three sites and also sampled for aquatic arthropods. Species richness tended to follow mean plant complexity. Individual abundance did not follow mean complexity but showed scale specific peaks. Adding a mismatched plastic form to a site resulted in scale specific changes to the fauna. The data suggest that *M. spicatum* supports a full evenly distributed fauna, while *V. americana* has a depauperate uneven fauna. *Hydrilla verticillata* supports an abundant fauna biased toward a few species in a particular size range. A predation shadow was defined as the point of transition from a small-scale linear region to a large-scale complex region. Box-counting plots show that predation shadows correspond to major structural features of the plants. Peaks in individual abundance or biomass corresponded with these regions. Distribution of species by mean body mass appears to be clumped with the number of clumps showing mean plant complexity. The data do not support the distribution of resources as a causal factor of community structure. The data are consistent with predation as a causal factor of community structure.

CHAPTER 1 INTRODUCTION

Of all the unanswered questions in science, the simplest ones are often the hardest to answer. In ecology, these questions usually take the form of "Why are there so many/so few of species (x) around here?" Occasionally, we can provide a simple answer to such a question. There are so many Asian Tiger mosquitoes because they breed inside the numerous discarded car tires. There are so few manatees because we hit them with boat propellers. Such answers are true but are also oversimplified, often to the point of being misleading. Usually, we have little or no idea why a given species occurs at the population level that it does.

In perhaps no other field of endeavor does this shortcoming have a greater impact than in the field of classical biological control. Biological control is usually defined as the control of a noxious species (plant or animal) through the actions of natural predators (DeBach and Rosen 1991). Classical biological control comes into play when the pest species is not native to the area but has become established and now causes a problem. The theory behind this is that the species is a problem in the new area because it has left its natural enemies behind and thus flourishes without them. If a species is declared a target of a biological control program, researchers will search its native ranges for any species that acts as a natural enemy of the target. Theoretically, such a natural enemy could serve as a biological control agent if released into the area where the target species is a pest.

When biological control is successful, it can be phenomenally successful. There are numerous examples of target species permanently reduced to non pest levels resulting in enormous savings of money in yearly pest control expenditures (Pimental 1965, van Lenteren 1980, DeBach and Rosen 1991). In the face of such obvious benefit and success, one may wonder why being unable to predict population levels of a species can be said to have a profound effect on biological control efforts. While applauding the numerous successes and not denigrating current research efforts, the fact remains that most intentional introductions fail for one reason or another. Summarizing data on the introduction of parasites and predators, van Lenteren (1980) found that only about one fourth of targeted pests were successfully controlled and that roughly the same ratio of agents could be said to be established at the site of release. In other words, three quarters of all targets failed to be controlled and three quarters of all introduced agents failed to establish. More recently, DeBach and Rosen (1991) summarized all data and found slightly better numbers. Of 416 species of insect pests targeted for biological control, 164 were at least partially controlled. Of the 4,226 species of natural enemies released, at least 1,251 could be said to have become established. The numbers were even better when the targeted pests were plant species. Of 125 species of weeds targeted for biological control, 49 were effectively controlled. Of 701 importations of control agents, 398 became successfully established in the wild.

Given that the food of the biological control agent is so abundant that we determine it to be a pest, why is it that so few species become established upon release into the wild? If we examine the procedure used to choose potential agents, we see that great effort goes into ensuring that the agent preferentially feeds on the target. Since the

pest species is in such great abundance, it becomes obvious that the introduced agent has no serious competitors for its preferred food. Great effort is made to ensure that the agent comes from climatic conditions similar to the area of release. Quarantine procedures are used to screen out harmful parasites and pathogens. Enough individuals of the agent are released into a localized enough spot so as to ensure the probability of continued reproduction. Why then do introductions fail?

One can never discount the possibility that the new area is lacking some biological factor that was present in the native range but missing in the introduced area. But just as one cannot discount a missing biological factor, neither can one assert its presence beforehand. Careful initial breeding and host range testing within the country of origin should be enough to catch any critical factors. Perhaps the introduced organism is having trouble finding its food in the new area. In the case of herbivorous agents being released against target plant species, this does not seem likely. Releases of herbivorous agents are made directly onto large patches of the pest plant and often they are restricted by cages (DeBach and Rosen 1991). Failure to find the target might be a factor in the case of predatory or parasitic agents being released against animal targets. It is possible that the target species is finding enough shelter amidst the structure of its surroundings so that even though it is numerous enough to be a pest, it is not numerous enough to be readily found by the biological control agent. Another possible explanation for failure to establish is that the structure of the surroundings provides so little protection that predators are decimating the agents.

For the purposes of this dissertation, let us call the structure of the surroundings the arena and define arena as the identifiable area in which at least one prey and one

predator species interact, at least potentially so. By this definition the arena can be as complex as a parasitic wasp searching the entire surface of a plant or as simple as water striders (Gerridae) hunting only at the water surface. This definition also isolates the complexity of the arena from the complexity of the trophic interactions occurring there. In other words, simple interaction could occur in complex places and complex interactions can occur in simple places. Ladybird beetles (Coccinellidae) hunting aphids on a complex plant located within a greenhouse would be an example of the former. While the plant may be structurally complex, there is a relatively straightforward relationship between predator and prey. An example of the latter situation could be represented by the water striders on the water surface. While the water surface is essentially two-dimensional and simple, the water striders must pick out what is prey while avoiding strikes from fish after the same prey and distinguishing the artificial fly cast on to the water to lure the fish.

If complexity of the arena influences the interaction between predator and prey, and if we can quantify the complexity of the arena, then we should be able to predict what the relative probability of surviving predation would be for a given species introduced into that arena. This suggests that predation, acting over an arena of given complexity, could structure the prey community by providing differential levels of enemy free space. Assuming that reproduction or immigration rates are not overpowering, those species afforded with maximal protection from that arena should achieve the greatest population levels and leave a depauperate fauna of species that are relatively exposed.

It was with these ideas in mind that the present study was begun. It was hoped that by understanding the structural complexity of plants, we could begin to predict the

vulnerability of an organism to predation before time and effort were invested in the study of its biology. The resulting reduction in time spent searching for and testing organisms doomed to failure would result in increased success rates for biological control programs. The choice of aquatic plants and organisms was based purely on convenience and a pre-existing familiarity of the organisms involved.

CHAPTER 2

REVIEW: COMPLEXITY AND COMMUNITY

Before we continue, a few definitions are in order. A predator is an animal that over the course of its life kills and eats numerous other animals. A parasitoid is an animal that feeds on one individual animal and generally kills it. A parasite is an animal that feeds upon one or more animals without killing them. A scavenger is an animal that feeds on dead animals killed by some other source. A prey item is any animal that has the potential of being killed and eaten by a predator. A host is any animal that has the potential of being fed upon by a parasitoid or a parasite. For the purposes of this dissertation, the term predator includes parasitoids but not parasites or scavengers. Prey includes the hosts of parasitoids but not parasite hosts or the food of scavengers. While it is acknowledged that plants may serve in any of the roles mentioned above, they are not considered here as active participants.

Do not be misled by previous sentence and assume that since plants are not considered here as active participants that they are not considered at all. The entire premise of this study is that the structural complexity of plants (along with inanimate objects) forms the arena that helps control the outcome of the drama between predator and prey. So this review begins with a consideration of how to measure the complexity of the arena. Specifically, the concept of dimension as a measure of complexity is developed. With this concept in place, this review continues on to consider the predator and prey as actors on this stage.

Arena

Clouds are not spheres, mountains are not cones, coastlines are not circles, and bark is not smooth, nor does lightning travel in a straight line.
Mandelbrot (1983)

Infinite Coastline

Lewis Fry Richardson was an eccentric scientist who was interested in the measurement of complexity. His specialty lay in asking deceptively simple questions such as "Does the wind possess a velocity?" and then using simple experiments to analyze them. He was reported to have studied the question of turbulence by dumping a sack of white turnips into the Cape Cod Canal. At one point he became interested in the roots of conflict between nations. He sought to examine the theory that the length of the border between two nations was proportional to the level of hostility they had previously exhibited to each other. He started gathering the data he needed by consulting the encyclopedias produced by the different countries and this is where he ran into a complication. Each country seemed to have a unique value for the length of common borders. Clearly something was amiss as even the poorest country could well afford an accurate survey of its national borders. How could two countries come up with different answers to the question of how long their common border was?

He began to make his own measurements using maps and a set of dividers. He set the dividers to the desired scale and carefully walked the dividers across the map, counting the number of steps needed to travel various borders and coastlines. An accurate estimate of the length of the border was obtained by multiplying the number of steps by the scale the dividers were set to. He then sought to increase the precision of the measurement by reducing the scale and taking finer steps with the dividers. When he did so, he found that the dividers captured more of the detail of the boundary and resulted in

a longer estimate of the border's length. In fact, the estimated length continued to increase and never converged to a single value no matter how fine he made the precision. Theoretically, if one could measure the boundaries with an infinitely fine precision then the boundaries would appear to be infinitely long.

Richardson had discovered that the apparent length of a boundary based on a natural feature such as a coastline, river, or mountain range, had no true length. The apparent length of such an object was strictly relative to the scale used to measure it. Furthermore, if the apparent length of such a boundary is plotted as a function of the scale used to measure it, the result is a straight line if plotted on a log-log graph (Fig. 1).

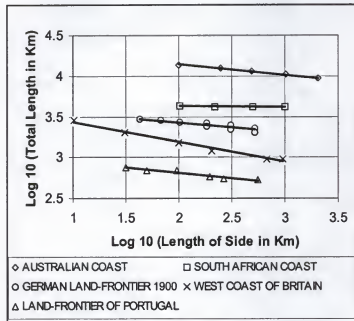


Figure 1. Length of national boundaries as a function of scale of measurement (Richardson 1961).

The exact relationship can be expressed as follows (using notation from Mandelbrot 1983):

$$L_{(e)} = \lambda F_e^{1-D}$$

Where F_{ϵ}^{1-D} intervals of length ϵ , are needed to approximate a boundary of length $L(\epsilon)$. The constant value δ is termed the unit length and represents the value of ϵ , when ϵ is equal to $L(\epsilon)$. Richardson did not proceed further with this work and all of these measurements and graphs were found among his papers after he died. The work was finally published posthumously (Richardson 1961) in an obscure Yearbook where it seemed doomed to be ignored.

Mathematics of Noise

Benoit B. Mandelbrot came across Richardson's paper and it crystallized many of the ideas he had been considering previously. Mandelbrot's forte was geometry and for several years he had been interested in long series of numbers representing the behavior of seemingly random events. One of his early works focused on the stock market and considered changes in commodity prices (Mandelbrot 1963). If someone wished to measure the total price change of a given commodity, then they would have to define when they took their measurements. Year-end prices were easy to obtain but missed much of the fluctuation. Daily prices required more vigilance yet they missed much of the rise and fall of prices that occurred over the course of the day. Before his work, brokers considered commodity prices to be driven by large-scale forces determining long-term trends. Small daily changes were considered to be independent of long-term trends and to be essentially random in nature. Mandelbrot discovered that the variability in prices was time independent and symmetrical across scale if one considered it logarithmically. In other words, the ratio of the number of price changes of size x to the number of price changes of size $10x$ was always the same no matter what time span was

considered and no matter how big x was. To put it mathematically, if the number of changes of size x could be written as N_x then the following formula would hold true;

$$\frac{N_x}{N_{10x}} = \frac{N_{10x}}{N_{100x}}$$

The distribution of commodity prices was self-similar, such that part of the graph looked just as complicated as the whole graph.

The idea of symmetry across scale was still fresh in his mind when he began to work on the problem of predicting errors in the transmission of computer information across phone lines. Static is an unavoidable feature of this kind of communication and while one can boost the signal strength to drown out the noise, there will always be an occasional burst of static large enough to cause an error in the flow of information. The distribution of these errors appeared to be random yet clustered. Mandelbrot (1965) realized that the distribution of these errors were analogous to the distribution of commodity price changes he had studied previously. If one examined a day where errors had occurred, then one could obtain a ratio of the number of hours with error-free transmission to the number of hours that contained at least one error. If one then looked at one of those hours that contained an error, you would get exactly the same ratio by comparing the number of minutes with error-free transmission to the number of minutes that contained at least one error. And again, if one then looked at one of those minutes that contained an error, one would get exactly the same ratio by comparing the number of seconds with error-free transmission to number of seconds that contained at least one error. The distribution was self-similar and independent of any time scale, exactly like the distribution of commodity price changes.

When Mandelbrot came across the paper by Richardson (1961) it all began to click into place. The abstract changes in the prices of cotton, the real-time electronic static interrupting a data stream, and the physical ruggedness of an actual coastline all exhibited the same qualities. A value that was thought to be real (total change in price, amount of error-free time, and length of coastline) was entirely relative to the scale of measurement. The complexity of the measured phenomena remained constant across a broad range of scales. This realization led to the proposal that the exponent D derived from Richardson's measurement of natural boundaries was in fact a dimension, as loosely defined by mathematical convention, although D can and often does hold a non-integer value. As defined, dimension became an expression of complexity. The very nature of D being a fractional dimension led Mandelbrot (1967) to coin the term Fractal Dimension (D_f).

Euclidean World and its Monsters

The idea that dimensions can be an expression of complexity is a little difficult to grasp. It might best be shown by first examining some of the classic objects in Euclidean geometry and their integer value dimensions. It is easy to think of a cube or sphere as being three-dimensional ($D = 3$) and a filled square or circle as being two-dimensional ($D = 2$). Without too much difficulty it would be easy to convince someone that a cube is more complicated than a square ($3 > 2$), and that both are more complicated than a straight line ($D = 1$). By final extension, all three objects would be more complicated than a single point ($D = 0$). The dimension of the object thus becomes a numerical value of its complexity.

Obviously, these perfect objects from Euclidean geometry do not occur in the real world. There are neither perfect circles nor straight lines in nature, but this is how we

have always modeled natural objects and events. We discuss point sources of pollution and square kilometers of a species range. We measure application rates for pesticides as so many liters per hectare. We measure the circumference of a tree trunk and calculate the volume of wood. We do these things even though we know there are no points, squares or circles in nature. We do these things because Euclid has provided us with a useful set of models with which to approximate the real world. While we never actually see these perfect shapes, it is comforting to know that in the theoretical world of pure mathematics, these objects are real and easy to analyze, yielding predictable results.

Be wary of what comfort you draw from this. Pure mathematics has also spawned objects that are just as real but have been impossible to analyze. Such objects bend logic to incredulity providing answers that we are not prepared to hear. These objects are the monsters of mathematics and they are also real.

One such monster is the Cantor set, first published by Georg Cantor in 1883 (in Peitgen *et al.* 1992). The best way to understand the Cantor set is to envision its construction (Fig. 2). Construction begins by imagining a line along the unit interval $[0,1]$. One then removes the open interval $(1/3,2/3)$ leaving behind two closed intervals $[0,1/3]$ and $[2/3,1]$ of length $1/3$ each. The next step is to take these remaining intervals and remove an open interval third from what is left of each. This results in four closed intervals of length $1/9$ each. This process is repeated so that after n iterations there are 2^n intervals of length $1/3^n$. This removal-procedure taking place an infinite number of times completes the set. The set of points remaining is the Cantor set. This strange set of points has an infinite number of members enclosed within a finite space and occupying no length. There is not the tiniest of intervals along the Cantor set that does not contain

empty space. If we wished to place the Cantor set in the sequence of complexity we discussed above we would have to say that it is less than a line ($D < 1$) but more than a point ($D > 0$). In other words, the Cantor set has a fractal dimension ($0 < D_f < 1$).

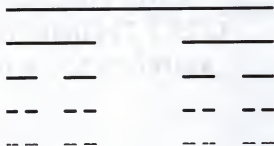


Figure 2. The first few steps towards creation of the Cantor set.

The next monster we need to examine is the Sierpinski gasket. Waclaw Sierpinski was a mathematician who published his now famous gasket in 1916 (in Peitgen *et al.* 1992). Construction of the Sierpinski gasket is similar to that of the Cantor set in that we begin with an object, perform a deletion function to it, and then repeat the process on the remaining parts an infinite number of times. However, instead of a line we begin with a filled in equilateral triangle. We divide the triangle into four equilateral triangles by drawing lines between the midpoints of the three sides. We then delete the middle triangle, leaving three triangles each $1/4$ the size of the original. This process is repeated on the remaining triangles so that after n iterations there are 3^n triangles, each of which is $1/4^n$ the size of the original. The gasket itself is created when this deletion process has been completed an infinite number of times. What is left is an object that has a perimeter but no area, being composed of an infinite number of holes (Fig. 3). The Sierpinski gasket is clearly more complicated than a line ($D > 1$) since the lines used to

define the original triangle are still in place, but it is also clearly less than a completely filled triangle ($D < 2$). The Sierpinski gasket also has a fractal dimension ($1 < D_f < 2$).

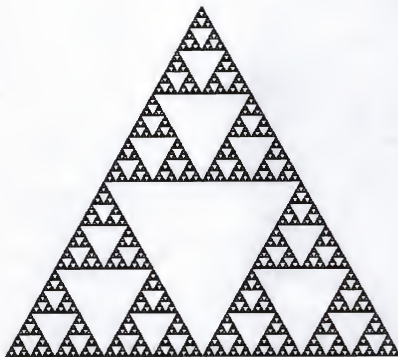


Figure 3. Sierpinski gasket approximation.

The last monster I wish to discuss is the Koch curve, first described by Helge von Koch in 1904 (in Peitgen *et al.* 1992). Unlike the previous two examples, adding to an object instead of deleting creates the Koch curve. One starts with a straight line and then divides it into three equal sections (Fig. 4). The middle section is replaced with an equilateral triangle missing its base. The resulting shape now has 4 line segments each of which is $1/3$ the length of the original. As before, this process is repeated so that after n iterations there are 4^n line segments, each of which is $1/3^n$ the size of the original. The Koch curve is achieved when this process has been completed an infinite number of

times. If one starts out with an equilateral triangle instead of a line, then this process creates a Koch island or Koch snowflake as it is sometimes called (Fig. 5). A Koch curve is not a curve in the sense of it being composed of smoothly bent lines. Rather, the Koch curve is all corners and cannot be differentiated. In other words, nowhere along its length is there a point that has a unique tangent. Furthermore, like the coastlines measured by Richardson (1961), a Koch curve is infinitely long. If we were to consider the Koch snowflake, then we need to rationalize an infinitely long border enclosing a finite space. While clearly more complicated than a line ($D > 1$), the Koch curve is a long way from filling the plane and so is also less than a filled circle ($D < 2$). The Koch curve also has a fractal dimension ($1 < D_f < 2$).

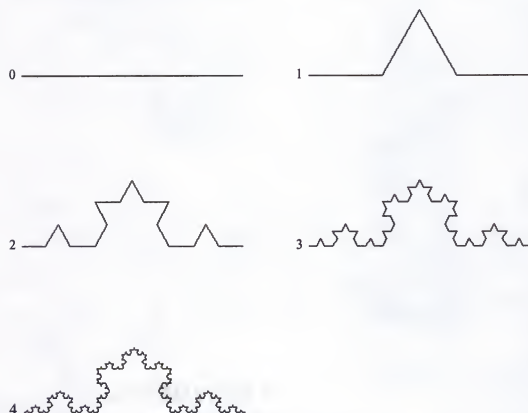


Figure 4. Four iterations towards the construction of the Koch curve.

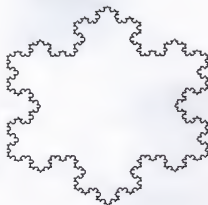


Figure 5. Approximation of the Koch snowflake.

Power Laws and a Multitude of Dimensions

The Cantor set, the Sierpinski gasket and the Koch curve are three examples of the many objects in geometry that seem to fall between the dimensions of Euclid. They defied rulers and tape measures and could not be counted. But slowly and in piecemeal fashion, mathematicians began to tame them through refinement of the concept of dimension. Or rather, mathematicians came up with numerous definitions of dimension. It is beyond the scope of this work to fully explore all the different possible dimensions. Discussion is limited to those immediately applicable to the problems at hand. Suffice it to say that each of these dimensions measures some subtly different component and how it scales relative to another aspect of the object being measured.

The roots to understanding dimension lie in realizing that most (but not all) are derived from the exponents of power law relationships. A power law is a relationship where the behavior of one variable behaves as a power of another. They take the generalized form of the following formula;

$$y = \lambda x^e$$

where δ is a constant and e is the exponent from which a dimension can be determined. This last point might best be shown by considering the power law formulae for the area of a circle and square.

$$\text{Area}_{(\text{circle})} = Br^2$$

$$\text{Area}_{(\text{square})} = s^2$$

For the circle, the area is dependent on a constant (B) multiplied by the radius raised to a power of 2. For the square the constant is 1 and the side length is raised to the power of 2. The area of these objects is a two-dimensional feature and the exponent is 2. The perimeter of these objects is one-dimensional and the formulae for perimeter involve an exponent equal to 1.

$$\text{Perimeter}_{(\text{circle})} = 2Br^1$$

$$\text{Perimeter}_{(\text{square})} = 4s^1$$

Similarly, the formulae for volume involve different constants, and r and s raised to the power of 3.

I wish to point out that there is not one true dimension for any object. Rather the same object can have numerous dimensions depending on which aspects are being measured. The above examples of the circle and square are relatively simple, yet they can simultaneously be Dimension one or Dimension two depending on whether one is measuring the perimeter or the area. Complex objects or groups of objects can have even more subtle distinctions and so great care must be taken to ensure that you are measuring the feature you are most interested in. In the case of the mathematical monsters discussed above, there are no simple formulae for perimeter or area and so their dimension is not intuitively obvious.

Measure of the Monsters

The theoretical groundwork for determining the dimension of a mathematical monster lay in the separate works of Carathéodory, Hausdorff and Besicovitch (in Mandelbrot 1983). Suppose you wished to evaluate the area of a planar shape S , a classical approach to doing so would be to cover the set with a collection of small squares. One could then approximate the area of S by multiplying the number of squares needed by the area of one square. Carathéodory reasoned that one was not always able to use known coordinates so he substituted discs for squares. He also avoided making the assumption that S is planar by using spheres, which are equivalent to discs in two-dimensional space. As one decreased the size of the spheres, the estimated area of a standard object (i.e. where D is an integer) would asymptotically approach its true value. Hausdorff realized that one did not need to know the dimension of the object beforehand. The dimension could be determined from the relationship between length and volume as measured by the spheres. If length is infinite and volume is zero, then the shape could only be two-dimensional. Besicovitch extended this argument to include dimensions of non-integer value. The resulting dimension is termed the Hausdorff-Besicovitch dimension (D_H).

The mathematics is complicated but the D_H can be defined from the limit

$$d = \lim_{r \rightarrow 0} \left(\frac{-\log N(r)}{\log r} \right)$$

where $N(r)$ is the minimum number of spheres of radius r needed to cover the object and d is equal to $1-D_H$ (Mandelbrot 1983). Rearranging this formula we get the following;

$$D_H = \lim_{r \rightarrow 0} \left(\frac{\log N(r)}{\log \left(\frac{1}{r} \right)} \right)$$

This formula is equivalent to the following power law

$$N(r) = \lambda r^{-d}$$

or

$$N(r) = \lambda r^{1-D_H}$$

where λ is a constant. We can determine d as the negative value of the slope of a log-log plot of the minimum number of spheres of radius r plotted as a function of r . Since this slope is already negative, a negative of a negative results in a positive value for d . The Hausdorff-Besicovitch dimension (D_H) can then be determined as $1-d$. Or, by using the second version of this formula we can say that D_H is equal to $1 -$ the slope of the log-log plot.

The problem is that there is no simple way to determine what the minimum number of spheres would be. To overcome this difficulty, mathematicians have developed the similarity dimension (D_s) as an estimate of D_H . While not a perfect match with D_H , D_s is easy to calculate for most mathematical objects. Like most dimensions, D_s is derived from a power law relationship. For D_s , the power law lies in the relationship between the number of pieces an object can be divided into (n), and the reduction factor (s).

$$n = \frac{1}{s^D}$$

or

$$D_s = \frac{\log n}{\log\left(\frac{1}{s}\right)}$$

If we take a straight line and divide it into 3 pieces ($n = 3$) we will have reduced the size of each piece to $1/3$ that of the original ($s = 1/3$). This means that for a straight line $D_s = 1$ since the following is true

$$3 = 1 / (1/3)^1$$

or

$$1 = \log 3 / \log (1/(1/3))$$

or

$$1 = \log 3 / \log 3$$

Similarly, if we take a square and divide it into 9 pieces ($n = 9$) we will have reduced the length of each side to $1/3$ that of the original square ($s = 1/3$). This means that for a square $D_s = 2$ since the following is true

$$9 = 1 / (1/3)^2$$

or

$$2 = \log 9 / \log (1/(1/3))$$

or

$$2 = \log 3^2 / \log 3$$

This is easily extended to the fractal objects we have already considered if we remember how they were constructed. During construction of the Cantor set, each iteration resulted in twice as many line segments ($n = 2$) each of which were $1/3$ the length of the original ($s = 1/3$). Thus for the Cantor set we arrive at the following value for D_s

$$D_s = \log 2 / \log (1/(1/3)) \cdot 0.6309$$

Similarly, during construction of the Sierpinski gasket, each iteration resulted in 3 times as many triangles each of which had sides 1/2 the length of the original ($n = 3$, $s=1/2$)

$$D_s = \log 3 / \log (1/(1/2)) \cdot 1.5850$$

and in constructing the Koch curve each iteration resulted in 4 times as many line segments each of which had sides 1/3 the length of the original ($n = 4$, $s = 1/3$)

$$D_s = \log 4 / \log (1/(1/3)) \cdot 1.2619$$

The end result is that we now have a simple way of estimating the dimension of any mathematical object as long as we have some idea of how it was created. The monsters remain bizarre, but they are now understandable and we can compare the complexity of one versus the other. One dark corner of pure mathematics has been illuminated, but how does this relate to measuring the length of a coastline?

Measure of Nature

Mandelbrot (1983) maintained that a plethora of natural objects and phenomena were fractal in nature. Theoretically then, natural objects should have non-integer D_H values. If we attempt to measure this, we again run into the problem of *a priori* determination of the minimum number of spheres needed to cover the object. Without this knowledge we cannot determine D_H . Neither can we easily determine D_s since natural objects do not have readily observable factors of reduction and replication.

Similarity dimension is based on the principle of self-similarity. If we examine the monsters in close detail, we note that each of the objects is composed of parts that resemble the whole. The Cantor set is composed of two parts that are an exact match to

the whole set except that each is $1/3$ the size of the whole. Each of these parts is itself composed of two copies $1/9$ the size of the whole. Similarly, the Koch curve and Sierpinski gasket are composed of reduced copies of themselves.

Natural objects such as coastlines are not self-similar in the sense of being composed of exact copies of themselves. However, as evidenced by Richardson's work with dividers, natural objects can maintain a constant level of complexity across a wide range of scales. This results in the previously described phenomena of a log linear increase in the apparent length of an object in response to a log decrease in scale of measurement. This so-called Richardson effect is what led Mandelbrot to coin the phrase fractal dimension in the first place. So that while a coastline cannot be said to be exactly self-similar, it can be described as statistically self-similar. The object resembles itself not in being an exact copy but in being just as complicated at all scales.

The problem with using dividers to estimate the dimension of an object (*sensu* Mandelbrot) is that the resultant counts are sensitive to the initial placement of the dividers. Also, the dividers cannot take into account a path that crosses itself or an object composed of disjoint parts. Neither can it measure the holes in an object. A more user-friendly method of measuring the dimension was needed.

The roots of a simpler method lay in the definition of another dimension, the so-called Minkowski-Bouligand dimension (D_M). This dimension is similar to D_H but is determined in a different manner (Schroeder 1991). To find the D_M of a curve, we let the center of a small circle with radius r follow along the curve. The area $F(r)$ that this circle sweeps out as it follows the curve is termed the Minkowski content or the Minkowski sausage. If we divide this area by $2r$ and allow r to approach zero, we begin to

asymptotically approach the length of the curve. If this curve is linear then this division of the Minkowski sausage approaches a finite value. If the curve is fractal in nature, then the estimated length never levels off but continues to increase. In fact, the rate of increase can be used to define D_M since the ratio of $F(r)/2r$ is proportional to r^{1-D_M} . If we wish to write out the entire formula, it would take the following form:

$$D_M = \lim_{r \rightarrow 0} \left(\frac{\log F(r)}{\log \left(\frac{1}{r} \right)} \right) + 2$$

It becomes immediately clear that the formula for D_M is close to that for the D_H . Instead of a count of minimal number of discs ($N(r)$) needed to cover an object, we use the area of the sausage ($F(r)$). This formula is no easier to use than the Hausdorff-Besicovitch dimension, but it intuitively led to a more easily determined dimension.

Mandelbrot (1983) pointed out that trying to measure D_M of an object like the coastline of Britain was like somebody laying an end-to-end line of rubber tires along the coast. You could then determine D_M by straightening the line of tires. The diameter of one tire multiplied by the number of tires needed results in the estimated length of the line and the diameter of a tire multiplied by the length gives us the area. It is then possible to determine D_M from the slope of a log-log plot of the area versus the diameter of the tire. By further extension, if we imagine that we are using squares instead of circles, then we can approximate D_M by overlaying the object with a grid and counting the number of boxes that contain a piece of the edge of the object. This technique is called mosaic amalgamation by Kaye (1989) but is more commonly referred to as the

box-counting or grid overlay method. The following formula can be used to obtain a dimension that is commonly called the box-counting dimension (D_B).

$$D_B = \lim_{s \rightarrow 0} \left(\frac{\log N(s)}{\log \left(\frac{1}{s} \right)} \right)$$

Note the similarity to the formula for D_H . The main difference being that D_B uses squares on a grid of side length s instead of circles of radius r . More importantly, instead of trying to determine the minimum number of circles that will completely cover an object ($N(r)$), D_B uses the relatively simple count of the number of squares that intersect the object.

Fractal Geometry of Nature

Mandelbrot (1983) declared that nature is fractal and with the tools of box-counting and dividers step-counting, a flurry of papers were published to show that indeed, nature was fractal. So far, fractals have piqued great interest among ecologists but few studies have tried to apply them. Most studies do not go beyond simple measuring and demonstration that fractals do occur in nature.

One area where fractals have been investigated more fully is the branching pattern of fungi cultures and plant roots with regards to the exploration and exploitation of the environment. Ritz and Crawford (1990) demonstrated that fungal colonies were fractal. They found that young cultures had a low dimension, which steadily rose as the culture aged. They hypothesized that a low dimension would be more effective in exploring the immediate environment but that to exploit a resource the fungi needed a more complicated pattern, i.e., higher dimension. Bolton and Boddy (1993) pursued this idea further by rearing different species of fungi on media of different nutrient quality.

Although the different fungal species had differing dimensions, they did exhibit the same trend with regard to nutrient level. High nutrient levels resulted in high dimension values for the fungal mycelia, while low nutrient levels led to lower dimension. Similar relationships have been found for the dimension of plant roots and nutrient level (Eghball *et al.* 1993; Lynch and van Beem 1993; Berntson 1994). Fitter and Stickland (1992) provided contradictory evidence measured from the roots of two species of grasses and two dicots. Using step counting, they found that the dimension of the roots increased with age but showed no relationship to nutrient level.

Plant structures other than the roots have been found to be fractal and this has led to useful applications in forest ecology. Taylor (1988) measured tree rings and found a fractal relationship between their variance and mean. He was able to detect changes in growth regime, although he was unable to correlate these with a particular cause. The crown of trees has been measured as fractal and found to be directly related to site quality and inversely related to the self-thinning tendency of mature trees (Zeide and Gresham 1991; Osawa 1995).

On a larger scale, much promise has been shown in the measurement of patches within the discipline of landscape ecology. Using satellite and aerial photographs, researchers have begun to understand and measure the impact of man on landscape-sized patterns. For example, Krummell *et al.* (in Milne 1988) found that dimension would be low at smaller scales. They postulated that the square shape of agricultural plots caused this. But general principles in landscape ecology have been few and far between. Wickham and Norton (1994) found that agriculture increased the dimension of wetlands.

Instead of imposing the linear shape of plots, agriculture fragmented the wetlands leading them to reflect larger landscape patterns.

Animal Community

Even though there have been few papers that deal with the animal community as it exists on a fractal surface, there have been many papers that look at the arena and how it influences animal communities. This section summarizes the literature that attempts to find the causal relationship between structure and community.

Passive Physical Response

Plant complexity can have a natural sorting action on the animal community that requires no other interaction. All other things being equal, large erect plants are easier to find and colonize than small plants and should therefore support larger population of invertebrates. Lawton (1986) reviewed published records of the insect fauna on British plants. He found that if one compares different plants with similar size ranges, the more complex one will have more species of insect on it. An alternative explanation lies in his definition of complexity, which included diversity of structural characteristics as well as the tendency to occupy space.

Diversity in plant structure can create new microhabitats resulting in an increased number of species. Tallamy and Denno (1979) demonstrated this. They examined two grass species for the structure of the sap-feeding invertebrate community on them. *Distichlis spicata* stems reach heights of 50 cm with stiff culms that tend to stay erect. Subsequently, this species forms a thick thatch layer. *Spartina alternifolia* stems reach heights of 10-40 cm with leaves that tend to be more divergent. Older leaves lie right on the marsh surface and rapidly decay. The thick thatch layer results in *D. spicata* having a

richer and more diverse fauna than *S. alternifolia*. If the thatch is removed, richness drops significantly but diversity and evenness fluctuate.

There does appear to be an impact on the arthropod community from the presence of a diverse understory. Stoner and Lewis (1985) examined the macro-crustacean community in seagrass beds, *Thalassia testudinum*, with an understory of calcareous algae, *Halimeda opuntia* (L.). Manipulative experiments involved the removal of one or both plant species. These resulted in no particular impact on arthropod numbers when compared as total number versus plant surface area, but there was a decided impact on particular species that were assumedly adapted to particular structures. Their conclusions suggest that total faunal abundance was a function of habitat surface area, but that the faunal diversity was a function of qualitative aspects of the area's surface.

Another possible passive impact on arthropods arises from the effect of plants on the wind and water currents around them. While, there does not appear to be any studies on the effect of plants on wind speed and subsequent colonization rates, the impact of plants on water currents and colonization rates has been clearly documented. Gregg and Rose (1985) sank trays of plants into unvegetated streams. The plant's impact on water velocity seemed to be the determining factor in what the resultant invertebrate fauna would be. Arthropod guilds were about equally represented in number regardless of type of plant cover, but the guilds were composed of different species. Unfortunately, no size comparisons were made. Dean and Connell (1987b) found similar results using plastic "algae" mats. They saw this as a sampling artifact in that their idea of increasing complexity included larger size as well as form. Bigger mats contained a greater number of invertebrates resulting in increased numbers of species. Gibbons (1988) showed that

sedimentation rates on artificial "algae" were profoundly affected by the size and shape of the fake plants and that diversity increases may be due to these effects. Kern and Taghon (1986) put forward a contrary view. They found that passive recruitment alone could not account for the abundance of harpacticoid copepods since the frequency distribution of some copepods late in the year was opposite to that found on the same plants early in the year.

Behavioral Response

It is possible for animals to actively choose the plant forms they inhabit aside from passively settling at the whim of physical factors. Stoner (1980) found that when three species of gammaridean amphipods were offered a choice between three species of seagrass, the clump of seagrass with the highest biomass was chosen. If biomass was equal, then the clump with the highest surface area was always chosen. If the biomass was close and all surface areas were equal, then no preference was shown. However, Stoner also found invertebrates did select for the densest plants (i.e., highest biomass per unit area).

Hacker and Steneck (1990) also examined the size abundance patterns of amphipods on algae. They found that the number and size of spaces between the fronds had a positive impact on larger amphipods but little effect on the smaller ones. Highly branched and thin filamentous algae supported larger populations of amphipods. This was especially apparent for the smaller amphipods. They compared these findings to laboratory experiments that utilized the same algae as well as artificial versions. These experiments excluded predation or food value, yet produced similar patterns as those found in the wild populations. They determined that the distribution of these amphipods on different algae types was the result of active choice rather than just a response to

differential predation rates. They did acknowledge that predation might be an ultimate factor in the habitat selection.

Fish also show active choice towards particular plant structures. Anderson (1994) found that the number of kelp perch, *Brachyistius frenatus* (Gill), showed a strong correlation with the canopy cover provided by the giant kelp, *Macrocystis pyrifera* (L.). The correlation was strongest for juveniles, which theoretically had more to fear from predators. Adult fish were more even in their distribution. Furthermore, if the canopy cover broke down, then the fish congregated in lower plant structures such as the fronds.

Positive taxis cannot be considered a universal cause of species distributions on plants. Norton and Benson (1983) found that in the wild, all amphipods on brown seaweed, *Sargassum muticum*, were more abundant on the distal well-illuminated portion of the plants, which maintained higher densities of diatoms. While this distribution seems adaptive, laboratory experiments showed that some amphipods were not attracted towards either *S. muticum* or diatoms. So, while all of these species have a similar distribution, this could not be attributed to a universal behavioral response of the amphipods. Dean and Connell (1987a,b) found that four common invertebrates showed positive taxis to increased biomass of algae but they made no preferential selections between algae species of the same biomass. Russo (1987) found that epiphytic amphipods showed no preference for any black nylon bottle brushes regardless of their complexities or mass.

Trophic/Energetic Response

The idea that the structure of the arena can have an impact on the trophic or energetic responses of animals has been expressed before. It has been suggested that increased structure leads to a greater number of distinct resources, i.e., niches, which

results in more species being able to coexist in a given area (MacArthur 1972; Pielou 1975; Whittaker 1975; and Pianka 1978). Smith (1972) postulated that increased habitat complexity allows for more ways for feeding strategies to differ. In a more indirect sense, it has been reasoned that increased complexity would allow for increased attachment sites for the food of the associated fauna (Abele 1974; and Hicks 1980).

Actual experiments on these concepts have proven to be sparse. August (1983) used principle component analysis to study the effect of vertical variation in habitat physiognomy (complexity) and horizontal variation in habitat form (heterogeneity) on various aspects of the small mammal community in a Venezuelan forest. Species richness showed a positive correlation with complexity but not with heterogeneity. This was likely due to guild expansion rather than addition of new guilds. Diversity, abundance, biomass, and evenness showed little correlation with either complexity or heterogeneity.

Lawton (1986) reviewed the literature on the impact of plant architecture on insect diversity. He focused on phytophagous insects, and his idea of complexity encompassed size of plant through space as well as variety of plant structures. Comparing different plants with geographic ranges of similar extent, the more complex plant will have more species of insects on it. There are two possible reasons for this; size *per se* and resource diversity. Both explanations are similar to theories employed in island biogeography. Size *per se* has already been discussed, i.e., larger plants are more visible and more likely to be colonized. But the literature also suggests that resource diversity will impact the animal community. Plants with a greater variety of resources will support a greater variety of herbivores. While some of the variety comes from non-

trophic reasons (e.g., microclimate variations, refuge sites, over-wintering sites, oviposition sites, *etc.*), a plant's tendency to occupy space does affect the trophic interactions of the animal community. Bigger and older plants can have a different assemblage of insects as compared to younger plants. For instance, wood-boring insects would not colonize a seedling. Plants do not get this increase in diversity if they are annuals.

Lawton (1986) goes on to promote the idea that the energetic relations of an insect interacting with the fractal dimension of plant surfaces as an explanation for the relative abundance of insect species. If plant surfaces are fractal, then small insects outnumber large insects not only because they take up less space but also because there is absolutely more living space at the smaller scale. It would be meaningless to say how much physical space an insect has available to it without stating the size of the insect.

The energetics part of Lawton's argument comes from the power laws of animal metabolism as put forward by Peters (1983). Because of the way an animal's metabolism changes with its body mass (W), the number of animals (N) able to be supported by a given unit of energy is proportional to $W^{-0.75}$ or $(L^3)^{-0.75}$ if one wishes to approximate with an animals length (L). This relationship means that if resources limit the number of individual animals living in an area, then there should be more little animals than big animals because each little animal uses less of these limiting resources. The power laws suggest that an order of magnitude decrease in animal length should result in density almost 178 times higher ($((0.1^3)^{-0.75} = 177.8)$). Lawton suggests that if the plant has fractal dimension, then the area perceived by a smaller animal would be greater than that perceived by the larger animal. By way of example, he shows that if the plant surface

had $D_f = 1.5$, then an order of magnitude reduction in scale of measurement would result in the apparent distance between two points on that plant increasing by a factor of 3.16. The perceived area would increase by a factor of 3.16^2 , or roughly one order of magnitude. The expected density of an animal 3 mm long should therefore be longer than that of an animal 3 cm long by a factor of 10 based on perceived area and an additional factor of about 178 based on metabolic demands. Data from Janzen (1973) and Morse et al. (1985) seem to support this.

What Lawton fails to discuss is exactly why the energy resources would be distributed in a fractal manner. Yes, the surface of the plant clearly shows the Richardson effect and appears to have more available surface when viewed by a smaller animal, but there is only so much resource material inherent in the plant. At any given instant, the volume of the plant is fixed and does not change regardless of the apparent size of the surface. The situation is analogous to the example of the Koch snowflake in which an infinite boundary surrounds a fixed volume. The energy resources in a plant are part of the fixed volume and not the subjective boundary. One would have to show that an animal was space limited in its access to resources in order for a fractal surface to impact on an animal's abundance in this manner. This is clearly not the case. So if an animal's abundance correlates to a plant's fractal dimension, then the answer as to why this occurs lies elsewhere.

Competition Response

While there are no studies that compare an area's complexity with the competition level between animal species, there are numerous studies that compare the level of competition between animals of particular sizes. In a landmark study Hutchinson (1959) compared linear measurements of some body part from sympatric species and animals.

What he found was that the ratio of the larger species to the smaller one had a mean value of approximately 1.3. Many ecologists leapt on this value and hailed it as an ecological constant. Soon numerous studies began to appear in the literature finding the 1.3 size ratio in a variety of communities. Roth (1981) pointed out that while many of these studies showed a similarity to Hutchinson's ratio, there was an almost universal lack of statistical validation to the perceived similarities. The studies varied in their definitions of sympatric and in the meaning of the ratio itself. The ratio has been called the mean, modal and optimum value for species coexistence. It has also been called the maximum ratio for successful coexistence as well as the proper sum of differences along all n axes of niche space. It could be argued that such diversity of approaches all find a value near 1.3 was evidence for a universal underlying principle but Roth (1981) discounts this as evidence. She points out that the sum of published studies is not a random sample since any study that failed to find a pattern would be less likely to be published.

Roth (1981) goes on to reexamine the work of Schoener (1965) to show the lack of fit with Hutchinson's ratio. Schoener gathered 410 ratios of bill sizes of sympatric bird species. When plotted, the distribution had a mean and mode that was considerably less than 1.3. In fact, the overall distribution most closely resembled a discrete approximation of an exponential distribution. This suggests that the ratio of bill sizes between sympatric birds was no different from a random value. Roth does go on to caution against dismissing the possibility of pattern existing in natural populations but she does stress the need for statistical verification of observed patterns.

Even if the value of 1.3 has no special significance, there is evidence that interspecific competition can structure the body sizes of species in a community. Bowers

and Brown (1982) examined the coexistence of granivorous desert rodents in three different North American deserts. They rejected the null hypothesis that the species body sizes were no different than random assemblages. Species of similar body size (body mass ratio < 1.5) coexisted locally and overlapped in geographic distribution less often than would have resulted from chance. Price (1983) developed a mathematical model that helped to explain this. The size of the rodent determined the size of the patch the rodent would use so that animals of different size classes could coexist by utilizing different sized patches of food.

Working on a much smaller yet a more numerous scale, Walter and Norton (1984) extracted and measured 20,000 oribatid mites of 85 different species. No minimal size difference was noted except for congeners. This implied that they do not compete, but there was a strong pattern between congeners implying that these do compete. Given that there was not much variation in the possible diet, the authors were uncertain what could lead to this type of pattern. They were certain that some sort of biological factor was involved, but the data seemed to suggest that exploitative competition was not it. Tonkyn and Cole (1986) found that comparative size ratios of competing species had limited value. They found that if one drew randomly from any distribution of animals and plotted a graph of the number of species versus their relative size ratios, what you get is a graph that is monotonically declining and concave up. If there were some special ratio between adjoining species, this graph would appear with peaks. Dean & Connell (1987c) examined 50 pairs of species of aquatic invertebrates for potential competitive interactions. None of the comparisons showed a significant negative correlation. They admit that seasonal changes in overall numbers could affect these results, but an

additional test showed that the presence of a potential competitor had no significant effect on the substrate choice of an introduced amphipod. Nelson (1979) found no evidence for significant interspecific competition in amphipod fauna found in seagrass beds. Coen et al. (1981) found some evidence for competition for shelter between two caridean shrimps, at least within a laboratory setting.

What these negative reports seem to have in common is that they all examine communities that are on rich or abundant resources. Kohler (1992) found that competition could be a significant structuring factor in an area where resources are limited. Two periphyton grazers, a caddisfly larva, *Glossosoma nigrior* Banks, and a mayfly naiad, *Baetis tricaudatus* Dodds, were examined in the lab and in the wild. They did not affect each other's survival, but they did have significant impact on each other's growth. In addition, exclusion of the caddisfly led to significant changes in the size structure of the other invertebrates

Succession in Time or Space

A lot of the observed successional changes in an animal community are simply a question of luck of colonization. Whichever animal species finds and exploits an area first has a decided edge in winning out. Robinson and Dickerson (1987) showed this to be the case, at least on a small scale. They took small jars and colonized them with algae and other microorganisms at specific rates and sequences. Four different stable communities arose depending on which species were added first and at what rate they were added. A follow up study (Robinson and Edgemon 1988) examined this in more detail, i.e., more species and stricter measurements of timing. They found that the invasion rate was most influential. The order of invasion had almost no effect but the timing between the invasions was highly significant. In other words, second place can

still be successful as long as you're not too early or too late. Not that post colonization factors of the arena cannot also influence communities. Chironomid colonization of wading pools was found to be dependent on substrate particle size and organic matter content and that this effect occurs because of differential survival of the eggs (Francis and Kane 1995). But the lottery of colonization, while modified, is still considered the main structuring feature.

In this view of succession, age of the arena and colonization rates are what structure the animal community. But plant structure clearly has an impact on the animal communities and a progressive change in plant structures is almost the definition of succession. Dean and Connell (1987a,b, c) envisioned a steadily changing animal community responding to the steady changes in the structure of the plant community. In their investigation of the fauna on marine algal clumps, invertebrate species richness and abundance steadily increased with successional stage in response to changes in algal structure even though the greatest variety of forms occurred at middle successional stages. This is a successional pattern where bare rock is first colonized by low biomass levels of flat and smooth species of algae, followed by intermediate biomass levels of numerous species of varying shape, and finally, dominated by a higher and taller species with few lower branches and more complex tops. Evenness of the invertebrate fauna remained constant throughout succession, while temporal variation declined and spatial variation remained constant. This is somewhat supported by Beckett *et al.* (1992) who found that the total abundance of aquatic invertebrates was positively correlated with deteriorating condition of the aquatic macrophyte *Potamogeton nodosus* Poirét. The authors suggest that this may be a response to plant age rather than condition. This seems

slightly antagonistic to the findings of Fowler (1985) who reported that the faunal composition and overall species richness was essentially the same for birch seedlings, saplings and trees. Possibly, this could indicate an important difference in the fauna of aquatic versus terrestrial habitats.

Faster change such as the seasonal growth pattern of plants can also impact the final animal community. Hargeby (1990) compared the invertebrate communities on two species of macroalgae growing in the same water body and having roughly the same plant form. One species dies off every winter and is dominated by fast colonizing chironomids. The other species forms more permanent patches and becomes dominated by slower colonizers like *Gammarus* spp. In other words, the yearly die off leaves the invertebrate community in a permanently early successional state.

Other authors have found successional impacts to be more of a step-function response to structure rather than a gradual shift in response to time. Hurd and Fagan (1992) found a good example of this. They examined the spider assemblages along a gradient of four temperate successional communities. Diversity, richness and evenness exhibited a dichotomy between herbaceous and woody communities rather than a progressive change. Diversity, richness and evenness were all higher in younger fields, and clearly showed a step-function response to successional stage.

The interpretation of animal responses to successional changes is further muddled by the idea that stability across time and space is scale dependant. Ogden and Ebersole (1981) found that artificial reef fish communities were variable if examined over short time periods or small areas. But if a study is expanded to cover large reefs or greater time spans, then a stable structure of species presence and abundance becomes apparent.

Murdoch *et al.* (1972) compared the plant species and structural diversity in old-field habitats with the species diversity of homopteran insects. Any correlation was weak if one considered 1-m² patches but strong if one considered the whole field.

Summary

So what can be said about the interaction between the arena and the animal community? Undeniably, the natural world has a variety of possible shapes. For a variety of possible reasons, animals have been shown to interact with those shapes in a manner that seems to dictate the frequency of animal size classes. Any fundamental laws controlling this interaction have proven to be elusive. Absolute statements regarding passive size sorting, animal choice, trophic responses, competition, or succession as size determining factors have proven to be case specific and are often contradictory.

The implication is that these are modifying factors instead of basic underlying principles and that some other factor is in action that is strong enough to override the effects of these other factors. There is no need to assume one underlying principle. Nature is complicated enough to present us with multiple structuring principles, any or all of which could influence species abundance. Nonetheless, any factor that acts in a near universal manner needs to be considered as a potential organizing force. Predation has a near universal impact. Predation comes to nearly every animal species, at some point in its life, and should be examined as a potential basic controlling factor of the animal community structure. The problem is that the interaction between predation and arena is poorly understood.

Box-counting techniques have been purported to quantify the complexity of the environment and so suggest themselves as a potential technique to evaluate the

relationships between arena and the animal community. However, if predation is the structuring force in an animal community then naïve measurements of the arena will not elicit much information on the structure of the animal community. First, we must understand how the structure of the arena affects the interaction between the predator and prey. Only once these mechanisms are known, can we begin to understand how they might shape a community of animals. So, if the techniques of fractal geometry can provide us with a framework for understanding the structure of the arena, we should be able to make objective measurements and predictions.

CHAPTER 3 PERCEPTION OF COMPLEX SURFACES

Box-counting has emerged as the most common method of measuring the dimension of objects. People who study chaotic dynamics have used it to measure the dimension of strange attractors. Ecologists have used it to measure the outline of habitat patches. Hydrologists have used it to measure water basins. And economists have used it to measure the fluctuation of prices over time. Yet no published guide exists on how to actually apply this technique. The result is haphazard application of different methods leading to often misleading or outright contradictory results. This has led to a backlash against fractal geometry as a tool in the natural sciences.

Rules for Box-Counting

"Then you should say what you mean," the March Hare went on. "I do," Alice hastily replied; "at least—at least I mean what I say—that's the same thing, you know." "Not the same thing a bit!" said the Hatter. "Why, you might as well say that 'I see what I eat' is the same thing as 'I eat what I see'!" Alice's Adventures in Wonderland, Lewis Carroll

Box-counting can be a sensitive measure of dimension but one must be careful on how it is applied. Subtle nuances in meaning for the words 'complexity' and 'dimension' have led to strange results. Nobody would trust the numbers provided by someone who uses a yardstick without understanding what 'straight' or 'length' really means, yet numerous papers have been published that utilize box-counting without defining their technique or what surface is being measured.

Apparent Dimension

Let us define an object's inherent complexity as the tendency for it to occupy space-time. In this view, a lake is more complex than a puddle because it occupies more space over a greater length of time. Furthermore, let us define an object's ecological complexity as the tendency to occupy space-time of that part of an object that interacts with another object or observer. So a seagull flying over a wave-tossed lake perceives one level of complexity, which is different from that of a fish, swimming in the lake, that is different again from that perceived by a benthic insect crawling along the bottom of that same lake. All three animals perceive a different level of complexity but the inherent complexity of the lake has not changed. What has changed is the level of interaction, or the surface that is being interacted with. How can box-counting dimension measure this complexity?

Consider the dimensions of classical objects of Euclidean geometry (D_E) and how a box-counting plot would appear if such perfect objects did occur. If we took a grid of squares and overlaid a perfect point ($D_E = 0$), the point would always fall in one and only one square. Remember that we determine D_B by using the following formulae introduced in the previous section,

$$D_B = \lim_{s \rightarrow 0} \left(\frac{\log N(s)}{\log \left(\frac{1}{s} \right)} \right)$$

We note that if $N(s)$ always equals one, then $\log N(s)$ always equals zero and thus for a perfect point $D_B = 0$. Next, imagine overlaying a grid on a perfect line ($D_E = 1$). If we cover this line with $N(s) = x$ grids, then $s = 1/x$ and therefore $1/s = x$. No matter how small we make s , D_B will always equal $\log x / \log x$, i.e., $D_B = 1$. Similarly, imagine

overlaying a grid on a perfect square ($D_E = 2$). If the side of the grid (s) were equal to the side of the square, then it would only take one grid to cover the square. If we reduce s to $1/2$, then it would take 4 grids to cover the square. If we reduce s to $1/3$, then it would take 9 grids to cover the square. No matter how small we make s , $N(s) = 1/s^2$, and therefore $D_B = \log(1/s^2) / \log(1/s) = 2$. Using similar arguments for a cube ($D_E = 3$), we find that $N(s) = 1/s^3$ and that $D_B = 3$. So, we see that for geometrically perfect (i.e. Euclidean) objects $D_B = D_E$.

Note that the plots can be expressed in units of length and area rather than the count of boxes. We can convert $N(s)$ into area by multiplying $N(s)$ by s^2 , and convert $N(s)$ into units of length by multiplying $N(s)$ by s . But these two values are not the same. Careful judgment must be made to ensure you are measuring the interaction you think you are measuring. Consider a disc drawn on a piece of paper. From the point of view of anything else on that paper, all interactions with the disc occur at the edges and the disc is indistinguishable from a circle. It is only when we rise above the surface of the paper that we can perceive the middle of the object and measure the area. So that while the disc has an inherent complexity of $D_B = D_E = 2$, anything interacting with that disc would find that it had an ecological complexity of $D_B = 1$, which is less than the Euclidean dimension ($D_E = 2$). The dimension used to create an object will be termed the Inherent Dimension (D_I), which is a fixed value for any given object or distribution. The ecological dimension can vary depending on how the object appears to a given observer so that it is here termed the Apparent Dimension (D_A). Box-counting dimension can be used to estimate either D_I or D_A . Any dimension derived from the formula used to create the object is D_I (e.g., area of a circle = πr^2 , $D = 2$). Any technique for measuring the

dimension of an object based on how that object is perceived is in fact measuring D_A (e.g., circumference of a circle = $2\pi r$, $D = 1$). D_A and D_I may be fractal or Euclidean or one of them may be fractal, while the other is Euclidean. This is not to say that D_I cannot be determined from D_A , only that they are related but different aspects of the object in question.

Minimum Size of Existence

So, with the cautionary explanation of the differences between inherent and ecological complexity out of the way, let us return to our thought experiments and consider what a box-counting plot would look like. Envision our previously considered perfect point. Euclidean geometry tells us that this object has a dimension of 0. It would be infinitely small and occupy only one point in space. Clearly, no such object exists in nature and it would be impossible to draw one. But imagine that we had such a point drawn on a piece of paper and we began to overlay it with our grid of squares. No matter how small we made the grid size (s), the point would always be covered by one and only one square. Our estimate of the size of the point would always be equal to the scale of measurement (s). There is of course, a small chance that the point would lay directly on the boundary between two grids, but if we assume our grid to be made up of perfect line segments, then this possibility approaches zero. A log-log plot of the estimated size of this point versus the scale of measurement (s) would have a slope of 1 and would intercept the x and y axis at the point [0,0]. Since this slope of 1 is equal to $(1-D_B)$, we see that the box-counting dimension is 0, and this accurately reflects the Euclidean dimension of a perfect point. Note, that for a perfect point $D_B = D_E = D_I = D_A = 0$.

The box-counting plot of a perfect point can be considered as a minimum line of existence. If an object exists, then it will intersect a minimum of one box. It is impossible to intersect less than one box. It is therefore impossible for an object to be measured as smaller than the scale of measurement. Only points above and to the left of the minimum line of existence can be measured. It is impossible to measure a point that lies below and to the right of the minimum line of existence (Fig. 6). This leads us to our first axiom about measuring objects with the grid-overlay method.

Axiom 1. No object can exist and be measured as being smaller than the minimum scale of measurement.

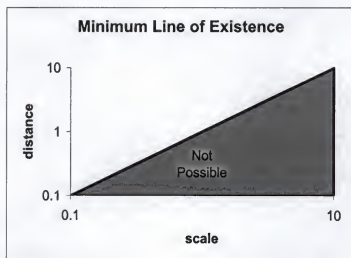


Figure 6. Box-counting plot of a perfect point.

We might be able to infer the size of an object smaller than the minimum scale of measurement, but we cannot measure it as such. A corollary to this axiom is that all objects smaller than the minimum scale of measurement are indistinguishable from points and that the size of a point will always be overestimated. Also, note that this axiom applies to all measurement systems, not just the grid-overlay method of box-counting.

All Things Are Relative

Let us now extend our thought experiment and consider a perfect line. By Euclidean definition a perfect line has dimension equal to 1, is perfectly straight, and stretches to infinity. If we had an infinitely large grid, we could overlay the line and count out an infinite number of squares that the line intersects. Changing the scale of the grid (s) results in there still being an infinite number of squares. This approach does not provide us with graphable data, and so we must consider this problem from a different angle. Imagine that we are flying along our perfect line in a rocket ship that is traveling at a constant velocity (v). If we travel for a set period of time (t), then we will encounter a set number of grid squares. Multiply that number of squares by s and we get an estimate of the distance we traveled. If we cut the scale of measurement in half, then we will encounter twice as many squares on our journey and the estimate of the length of travel is unaffected. In fact, no matter how we change s , the apparent distance traveled is constant. While changing velocity and the time period does affect the distance traveled, this distance is always a constant with respect to s . A log-log plot of estimated distance versus scale has a slope of 0 and therefore $D_B = 1$. Note that for a perfect line $D_B = D_E = D_I = D_A = 1$. Similar logic will show that a perfect plane has a slope of -1 , and therefore $D_B = 2$. Note, for a perfect plane $D_B = D_E = D_I = D_A = 2$.

But what about measuring real objects? The curious thing about real objects is that they are not equally complex at all levels of scale. The point, line and plane are unusual objects in that they involve infinities. The point is infinitely small, while the line and plane stretch out to infinity. Box-counting plots for these objects have constant slopes at all scales from 0 to 4. Such is not the case for objects of finite size. Let us

consider a perfect square with each side length equal to one hypothetical unit. The box-counting plot of this square is shown in Figure 7. Moving to the left of the plot (decreasing scale), we see that the line is asymptotically approaching an estimated perimeter of four and that the slope is becoming 0. For reasons that will be discussed later, this estimate of perimeter is always an overestimate except at $s = 0$. We conclude from the slope that the box-counting dimension of a perfect square is 1 since D_B is defined as $s \rightarrow 0$. The slope of this graph is never 0 except at $s = 0$. At scales larger than 0, the slope becomes increasingly different from 0. At first, the slope is slightly positive but as s approaches 1, the slope levels off and becomes negative. The implication is that at $s = 0$, the circle is clearly a line ($D_B = 1$). As s increases, the slope is slightly positive indicating that the circle is finite compared to a perfect line ($D_B < 1$). With increasing scale, the slope becomes negative, reflecting its two dimensional nature ($D_B > 1$). When s exceeds the size of the circle, the slope is positive again and the circle begins to resemble a point ($D_B = 0$).

A circle appears to have a fractional dimension at larger scales. This apparent fractal nature of linear objects measured under large scales has been noticed before. It is termed a "fractal rabbit" and has previously been dismissed as an artifact of the technique (Kaye 1989). But it becomes an intriguing idea if this phenomenon is more than a mere artifact. What if this apparent complexity is in fact an accurate representation of our perception of the object? A square is intuitively more complex than a straight line. Added information is required to bend that straight line in on itself to form the square. For years, people imagined that the world was flat. If we increase our scale of observation by moving higher into the air, we begin to perceive the curvature until finally

the world appears to be a sphere. Our perception of the complexity of objects is scale dependent.

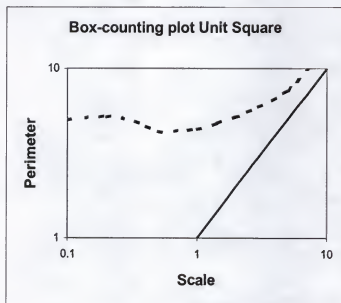


Figure 7. Box-counting plot of a perfect square with side length of 1 unit (— minimum line of existence; - - estimated perimeter of square).

At the largest scales of observation, the apparent complexity of the square levels off and the box-counting plot of a square asymptotically approaches the minimum line of existence (Fig. 7). The interpretation of this behavior is that at small scales one does not capture the angles of the square in the analysis and the square appears little different from a straight line. As the scale increases, more of the angles are captured in each box and the apparent complexity increases as we begin to appreciate the two dimensional nature of a square. As the scale continues to increase, it becomes easier to consider the square as a single point in space and the apparent complexity drops and continues to drop until the object becomes indistinguishable from a perfect point. In fact, this behavior was

alluded to as a corollary of axiom one. If no object can be measured as being smaller than the scale of measurement, then all objects appear to be points if the scale of measurement is larger than the object. Mandelbrot (1983) used the analogy of a ball of string to point out that the dimension of a real object can change depending on how far away one is from the object. Viewed at from a great distance, our ball of string appears to be no more than a point ($D_E = 0$). Moving closer, we see the ball has width, height, and depth ($D_E = 3$). Even closer, we see that the ball has texture, and eventually we would see that the ball is composed of lines of string ($D_E = 1$), which can appear to be small columns ($D_E = 3$). The same object has a varying D_E depending on scale of observation, in this case defined as distance from the object. If we were persistent, we could count $N(s)$ at scales as small as the individual fibers and since D_B is defined at the limit as s approaches zero, we might conclude that a ball of string is no more complex than a strand of hair. This approach would lose all information about complexity at larger scales.

The solution would be to use the Apparent Dimension (D_A) to describe complexity at these larger scales. We had previously defined D_A of an object as being relative to the surface of interaction. We can also define it as being relative to the scale of interaction across that surface. In other words, whereas D_B was defined at the limit as s approaches zero, D_A can be defined using the derivative with respect to s .

$$D_A = 1 - \frac{d(\text{length})}{d(\text{scale})}$$

Defining D_A as being relative to scale of observation results in ecological complexity having no intrinsic meaning without reference to scale or range of scales. This is important enough to be called axiom 2.

Axiom 2. The ecological complexity of an object and its measure (D_A) are strictly relative to the scale of observation.

Since no other dimension is defined as being scale specific, any D shown with reference to any scale greater than zero can be assumed to be D_A and the subscript A may be dropped for convenience sake (e.g., $D[1 \text{ to } 5\text{mm}] = D_A[1 \text{ to } 5 \text{ mm}]$).

Rule of Averaging

Now that we have determined D_A to be measurable at any scale, we run into the question as to whether to use minimum $N(s)$ or mean $N(s)$ to plot our graphs. A convenient feature about objects that extend or contract to infinity is that these two values are always equal. But for objects with finite size, $N(s)$ is not only a function of s but can also vary based on the orientation of the object relative to the grid. By definition, the minimum value of $N(s)$ needs to be used to plot the dimension but there is no known way to predict minimum $N(s)$ for an object with a complex shape. As previously discussed, box-counting dimension was developed as an alternative to Hausdorff dimension because it was difficult to determine the minimum number of circles needed to cover an object. The implication is that box-counting uses an average number of squares since it was developed as an estimate of the undeterminable minimum number of circles needed to cover an object. Minimum $N(s)$ can be extremely difficult to find for a complex shape, and so most researchers use mean $N(s)$ without worrying about potential differences. Most of the time, mean $N(s)$ will produce the same results as minimum $N(s)$ except at scales near where two different scaling regions meet. Minimum $N(s)$ produces a sharp transition between scaling regions while mean $N(s)$ results in an asymptotic shift between regions.

This behavior might best be shown by considering box-counting plots of simple objects using both minimum $N(s)$ and mean $N(s)$. Figure 8 illustrates the box-counting plot of two points separated by some unit distance $x = 1$. The longest distance within a grid cell is a diagonal cross-section. As long as this cross-section is smaller than the distance x , there is no way that the two points can fall in the same grid and $N(s)$ always equals 2 and the estimated size of the two points is $2s$. As soon as that cross-section exceeds x , then minimum $N(s)$ will always be 1 and the estimated size of the two points will be $1s$. If we use mean $N(s)$, then there is still a chance that the two points will fall into two separate grid cells. This probability decreases with increasing s and so the estimated size of the two points asymptotically approaches the minimum line of existence.

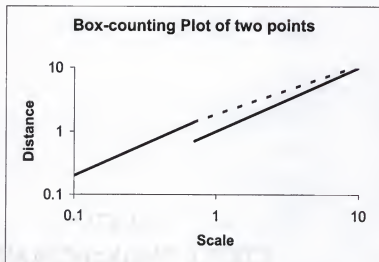


Figure 8. Box-counting plot of two points set a unit distance apart. The solid line represents the minimum determined distance and the dotted line represents the mean determined distance.

Another thing to consider when working with minimum $N(s)$ is that s needs to be equal to $1/n$ the size of the object being measured, where n is an integer. Reconsider the

box-counting plot of a unit square, but this time include the distance determined from minimum $N(s)$ as well as mean $N(s)$ (Fig. 9). We see that the minimum $N(s)$ plot resembles a series of octaves of regions with apparently increasing length. This happens because if the size of the object being measured is not a multiple of s sized grids, then one whole grid square is used to account for the fraction of length left over. Thus if we estimate length by multiplying minimum $N(s)$ by s , we steadily overestimate length unless the object is a whole number multiple of s . Note that mean $N(s)$ produces a smooth continuous line.

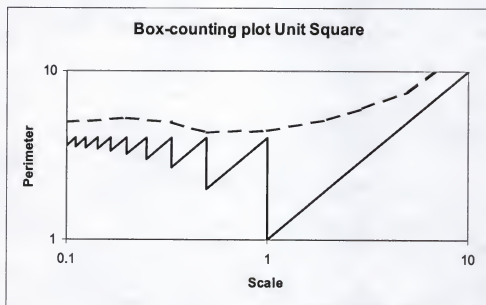


Figure 9. Box-counting plot of a unit square. The solid line represents the minimum determined distance and the dashed line represents the mean determined distance.

Whether to use minimum $N(s)$ or mean $N(s)$ should be decided with great care and with careful consideration of exactly what it is that you wish to measure. If one is interested in the exact structure of an object and knowing at exactly what point of scale

that the complexity begins to change, then one should use $\min N(s)$. If on the other hand, one wishes to study interactions across a complex surface and how probabilities are affected by changes in structure, then one should use $\text{mean } N(s)$. To date, the only evidence to support this assertion is anecdotal. Imagine watching an object disappear into the distance. The object does not suddenly shift from a three dimensional object to a zero dimensional object. Rather, there is a gradual transition in size until the object begins to be too small to be seen. An observer would probably lose the object for a moment, as the probability of detecting it becomes low, possibly regaining it, only to eventually lose it completely. Minnaert (1954), who pointed out that colors begin to blend and merge as they are viewed from further away, expressed a sense of this averaging of perception. Thus Minnaert points out that dandelions on a lawn will appear to be a green-yellow mixture and that apple blossoms will appear dirty white when viewed at great distances. The averaging of perception also seems to be related to the ecological approach to perception founded by Gibson (pg. 25-26 in Goldstein 1989). Without going too deep into the topic of mind and perception, the ecological approach states that we do not perceive static images, but rather we perceive objects dynamically through time and movement. While both Minnaert and Gibson were talking about vision, this concept should extend to any interaction.

Axiom 3. The probable outcome of an interaction is determined as a continuous averaging function across scale.

In other words, the probability of an outcome is the integration of its ecological complexity across all scales of interaction. This statement appears to hold true whether the interaction is the $\text{mean } N(s)$ value from a grid-overlay, a visual inspection of an

object, or a physical interaction across a complex surface. This can be shown by imagining a tall tree trunk growing straight. At a far distance we can only examine this tree at a large scale and it appears smooth edged. If we stick our nose right on the bark, we restrict our interaction to small scales and we can only see the complex surface. If we step back far enough to see the extent of the trunk and yet still notice the bark, we see that it is both smooth and rough with a continuous transition between them. We can say that it is smooth at this one large scale or that it is rough at this one small scale but we cannot pick a particular scale where rough becomes smooth. Theoretically, one could devise a scenario wherein a perfectly smooth surface had rough features below a certain resolution limit, but in the real world, such distinct boundaries do not exist. Now imagine that we are bouncing a ball off of the tree trunk. Providing that it is a large ball, the rebound will be predictable. On the other hand, a small ball would catch the irregularities of the bark and fly off in an unpredictable direction. Gradually increasing the size of the ball will gradually increase the predictability, but there will never be a sudden shift in probability. Thus, we see that D_A , our visual inspection of the tree, and the probable outcome of physically rebounding objects off of it all show continuous shifts between different zones of complexity

Testing Real-World Validity

The three axioms developed in the preceding section have profound implications for our understanding of interactions. If valid, they imply that we will be able to *a priori* determine the probable outcome of an event providing that the event is based on the shape of the object. In the instance of this dissertation, the event we are interested in is the perception of a plant's complexity by an animal observer. The rest of this section will

present an experiment designed to show that box-counting, when looked at with an appreciation of the three axioms already discussed, can be used as a fair and objective measure of the human perception of complexity.

Introduction

By definition, box-counting provides a number that is a dimension (D_B). What people have assumed is that D_B is immediately translatable as complexity. But the term complexity is highly subjective even if we remain within an anthropomorphic point of view. Human beings, at least, have little difficulty in comparing two objects and deciding which is more complicated. This does not mean that all people are in complete agreement. All observers may unanimously separate the extremes of a series but neighboring objects in a series can be judged quite differently. While proponents of box-counting argue that it provides us with a means of transcending the subjectivity, no one has tested the validity of the technique as a measure of subjective impressions.

This experiment will attempt to show that the perception of complexity is measurable by box-counting and that the view of the environment is quantifiable in an objective manner. While some may argue that human beings might not be a good model species for making universal claims about animal perception, they do have the distinct advantage of being able to tell us their opinion. To this end, I provided a set of images and ask people to evaluate the complexity of the individual images. I then measured the images using box-counting techniques and compared the subjective human response with the calculated values.

Materials and Methods

The choice was made to work with aquatic plants based solely on the author's preexisting familiarity with the flora and fauna of aquatic environments. The twelve

species listed in Table 1 were chosen because they are all common Florida plants representing a diverse array of forms, yet all growing fully submersed and rooted to the substrate.

Table 1: List of plant species used to create images.

Hydrocharitaceae	<i>Egeria densa</i> Planch.
	<i>Hydrilla verticillata</i> (L.f.)
	<i>Vallisneria americana</i> Michx.
Najadaceae	<i>Najas guadalupensis</i> (Spreng.) Magnus
	<i>Najas marina</i> L.
Potamogetonaceae	<i>Potamogeton illinoensis</i> Morong
	<i>Potamogeton pusillus</i> L.
Ruppiaaceae	<i>Ruppia maritima</i> L.
Ceratophyllaceae	<i>Ceratophyllum demersum</i> L.
Haloragaceae	<i>Myriophyllum spicatum</i> L.
Lentibulariaceae	<i>Utricularia inflata</i> Walt.
Scrophulariaceae	<i>Bacopa caroliniana</i> (Walt.) Robins.

Due to the inherent difficulty in three-dimensional imaging, two-dimensional approximations were used. Pressed and dried specimens of the above species were obtained from the Division of Plant Industry Herbarium, Florida Department of Agriculture and Consumer Services, Doyle Connor Building, in Gainesville, Florida. The herbarium pages were directly scanned using a Desk Scan II and were saved as PCX files. The image type was as black and white drawings with a resolution of 150 dpi x 150 dpi. The resulting images were then imported into Corel Paint ® and cleaned up so that all pixels within the outline of the plant were given values of 256 and all pixels outside the outline of the plant were given values of zero. The final images were printed at 100% scaling and were individually mounted on poster board for ease of handling.

Each plant was thus represented by a single image saved in two formats. There was a hard copy for visual evaluation and subjective rating as well as an electronic file copy for measuring by computer. Figure 10 shows the hard copy images at reduced scale.

Visual evaluation of these images was performed through the use of an informal survey. Staff and students from The University of Florida, Department of Entomology & Nematology, as well as the Department of Zoology were asked to participate. The pool of respondents was well mixed by age, race and gender but represented a biologically informed group of people. Each respondent was presented with the twelve boards containing the prepared images and asked to rate their complexity on a scale from 1 to 10, with 10 being the most complex. The respondents were told that they did not have to utilize all the numbers but could if they wanted to, and that ties were allowed. Respondents were questioned singly and given unlimited time to make their decisions. Complexity was not defined for them and no information as to the identification of the plants represented was provided.

Computer measurement of the images was more difficult than imagined. Available programs that purport to measure the fractal dimension of an image were inadequate. Most of them would count all pixels within the image and not just the edges of the object being measured, thereby failing to measure the apparent dimension of the object. All of them produced a single value "D" regardless of the scale of measurement and none of them could be calibrated to give values for specific scales of measurement. New programs had to be written.



A.



B.



C.



D.

Figure 10. Final prepared images of plant forms for box-counting and survey comparisons (not to scale). A) *Elodea densa*, B) *Hydrilla verticillata*, C) *Vallisneria americana*, and D) *Najas guadalupensis*.



E.



F.



G.



H.

Figure 10 (Continued). E) *Najas marina*, F) *Potamogeton illinoensis*, G) *Potamogeton pusilus*, and H) *Ruppia maritima*.



I.



J.



K.



L.

Figure 10 (Continued). I) *Ceratophyllum demersum*, J) *Myriophyllum spicatum*, K) *Utricularia inflata*, and L) *Bacopa caroliniana*.

The end result was two Matlab® computer programs that together provided two matched vectors. One vector is a list of counts of boxes that the edge of the object intersects, and the second vector is the scale of measurement (in mm) that resulted in that count. Program codes are included in the Appendix. These programs take the image and convert it to binary values where "1" represents a pixel on the object and "0" represents a pixel off the object. The programs then convert this image to a second image where only pixels on the edge of the object have a value of "1" and all other pixels are assigned a value of "0" (Fig. 11). Given the image resolution as input, the program calculates the size of one pixel in mm. It then divides the image into a matrix of n by n pixels and counts the number of squares that contain part of the image. The scale is matched to this count by multiplying the size of one pixel by n . The value of n is increased each iteration from 1 through 300 pixels. The number of grids containing positive values is tallied after each iteration. These tallies are appended to form a vector representing $N(s)$ at scales ranging from 1 by 1 through 300 by 300 pixels.

The diagram shows a transformation of a binary image. On the left is the original image, a 30x30 grid of 0s and 1s where 1s form a noisy, thick representation of an object's edge. An arrow points to the right, where the resulting image is shown. This second 30x30 grid contains 1s only at the precise edges of the object, with all other pixels being 0, representing a clean edge detection.

Figure 11. Diagrammatic representation of image preparation performed by Matlab program "yne.m".

Results

Human evaluation of the plant images showed some variability but overall was fairly consistent (Table 2). Standard deviation was lowest on those images judged to have either low or high complexity. Responses to images judged to have intermediate complexity showed the highest standard deviations. The data is better appreciated graphically (Fig. 12).

Table 2: Response to survey on image complexity (N = 15).

Species	Mean	Standard Deviation
<i>Bacopa caroliniana</i>	2.60	1.18
<i>Vallisneria americana</i>	2.80	1.26
<i>Potamogeton illinoensis</i>	3.67	1.40
<i>Potamogeton pusillus</i>	4.07	1.79
<i>Najas guadalupensis</i>	4.87	1.73
<i>Egeria densa</i>	4.87	2.07
<i>Najas marina</i>	5.07	1.62
<i>Hydrilla verticillata</i>	5.07	1.75
<i>Ruppia maritima</i>	5.60	2.26
<i>Ceratophyllum demersum</i>	7.60	1.59
<i>Myriophyllum spicatum</i>	8.00	1.41
<i>Utricularia inflata</i>	8.20	1.61

Box-counting data from the computer outputs was collected and distances of the images edges determined by multiplying the count ($N(s)$) by the scale of measurement (s). Graphing distance as a function of scale on a log-log plot results in the standard box-counting plots developed as the standard in determining fractal dimension (D_f) (Fig. 13). It is readily apparent that none of the plant images represents a truly fractal object since all of them approach a linear slope of zero ($D_f = 1$) at small scales. At larger scales, all of

the images increase in complexity at image specific rates. Slopes of these graphs were estimated and apparent dimension plotted as a function of scale (Fig. 14). The mean response was plotted as a function of the maximum-recorded D_A (Fig. 15). The resulting R^2 value was low at 0.465, meaning that maximum dimension was a poor predictor of human response to complexity.

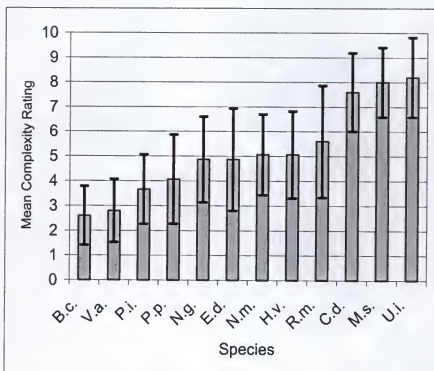
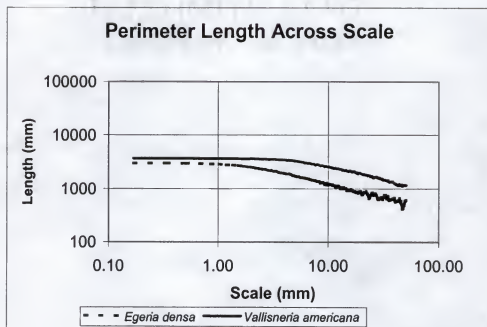
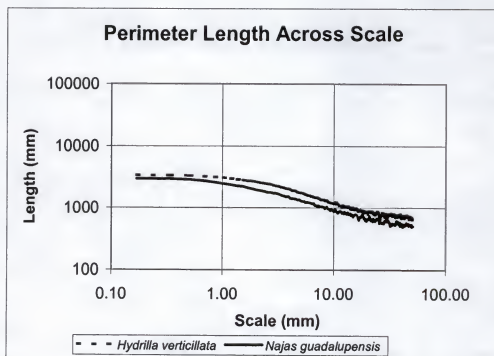


Figure 12. Mean response from opinion poll on complexity of plant images. Error bars represent $\pm$ one standard deviation. B.c. = *Bacopa caroliniana*, V.a. = *Vallisneria americana*, P.i. = *Potamogeton illinoensis*, P.p. = *P. pusillus*, N.g. = *Najas guadalupensis*, E.d. = *Egeria densa*, N.m. = *N. marina*, H.v. = *Hydrilla verticillata*, R.m. = *Ruppia maritima*, C.d. = *Ceratophyllum demersum*, M.s. = *Myriophyllum spicatum*, and U.i. = *Utricularia inflata*.

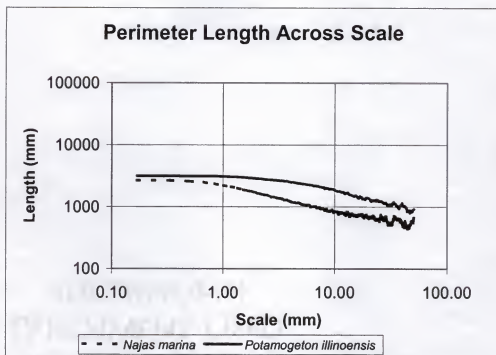


A.

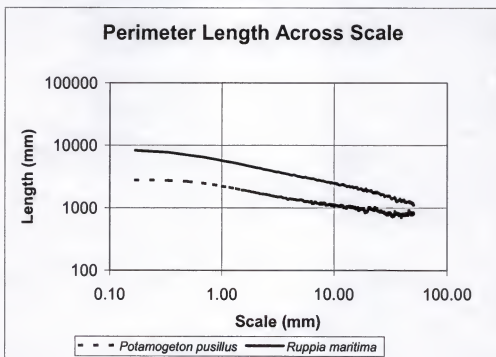


B.

Figure 13. Estimated length of perimeter of plant images across scale. A. *Egeria densa* and *Vallisneria americana*. B. *Hydrilla verticillata* and *Najas guadalupensis*.

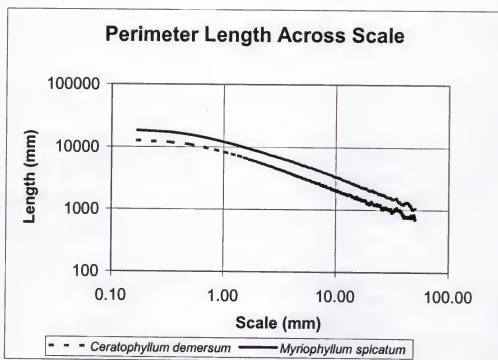


C.

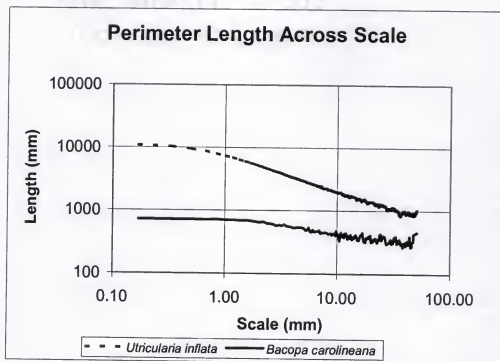


D.

Figure 13 (Continued). Estimated length of perimeter of plant images across scale. C. *Najas marina* and *Potamogeton illinoensis*. B. *Potamogeton pusillus* and *Ruppia maritima*.

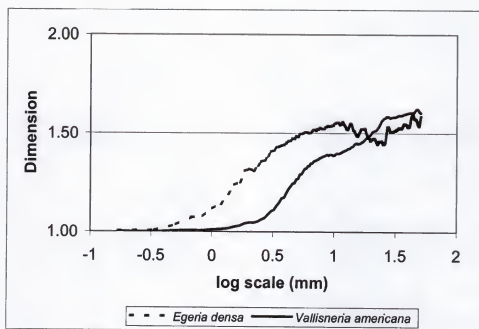


E.

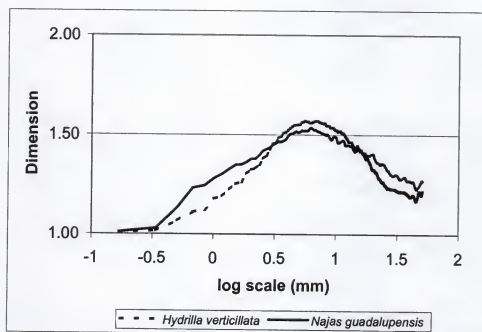


F.

Figure 13 (Continued). Estimated length of perimeter of plant images across scale. E. *Ceratophyllum demersum* and *Myriophyllum spicatum*. F. *Utricularia inflata* and *Bacopa carolineana*.

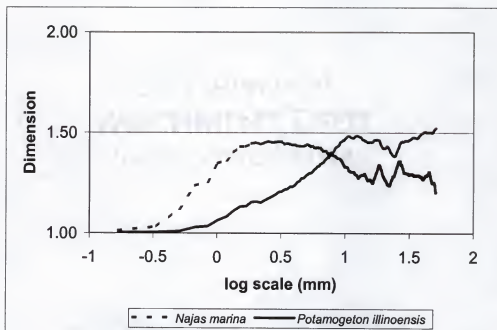


A.

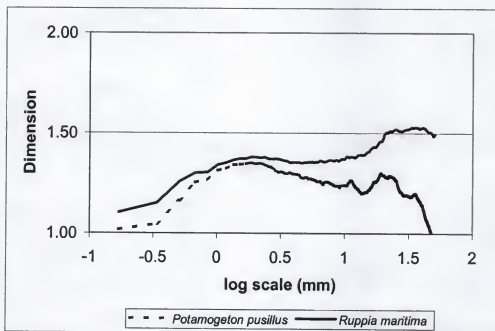


B.

Figure 14. Apparent dimension of perimeter of plant images across scale. A. *Egeria densa* and *Vallisneria americana*. B. *Hydrilla verticillata* and *Najas guadalupensis*.

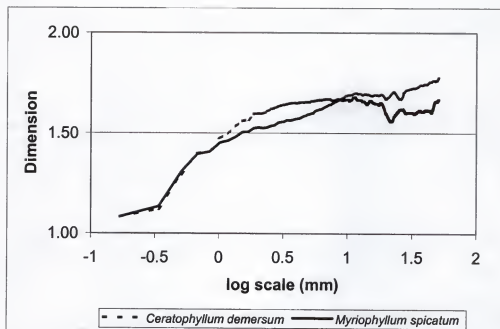


C.

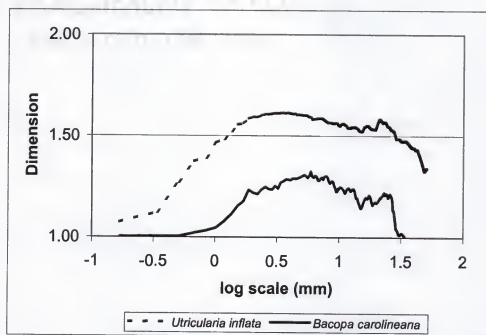


D.

Figure 14 (Continued). Apparent dimension of perimeter of plant images across scale. C. *Najas marina* and *Potamogeton illinoensis*. B. *Potamogeton pusillus* and *Ruppia maritima*.



E.



F.

Figure 14 (Continued). E. *Ceratophyllum demersum* and *Myriophyllum spicatum*. F. *Utricularia inflata* and *Bacopa carolineana*.

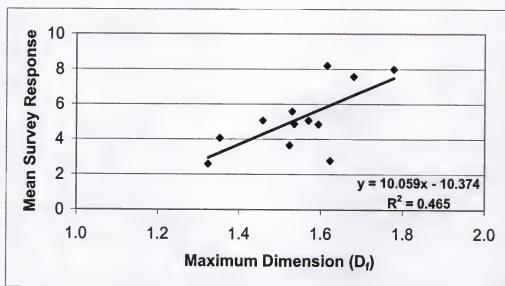


Figure 15. Mean human estimate of image complexity as a function of the maximum apparent dimension.

Discussion

Even though the maximum D_f represents the highest level of complexity that an object reaches, it is a poor predictor of the perception of complexity. A quick glance through the graphs displayed in Figure 14 shows why. Each plant's image has a seemingly unique pattern to the rise and fall of the complexity. Some images are steadily complex over the entire range of scales, while others are simple for the most part with only a peak in complexity. Maximum D_f will not capture this distinction. If an overall evaluation of complexity is needed, then mean D_f would provide more information.

Mean D_f is easily approximated as 1 - the slope of the $\log(\text{distance}) \log(\text{scale})$ plot (Fig. 13). The slope can be read directly from these graphs but it is more easily determined by converting all values for distance at scale to their log equivalents. The mean slope is then determined as the difference between the highest log distance value

and the lowest log distance value, all divided by the difference between log scales at those distances. Plotting the mean survey value for the human response as a function of the mean D_f proved to be highly significant with an R^2 value of 0.958 (Fig. 16). This is highly predictive and provides strong support for the notion that people perceive overall complexity to be the average across all scales and that box-counting is a good tool for measuring this.

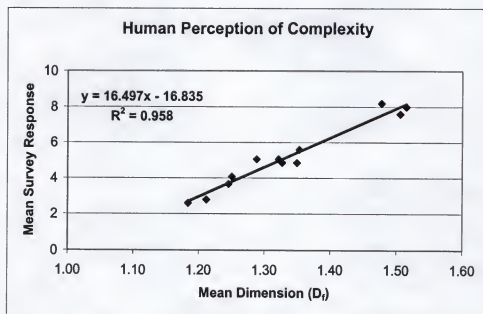


Figure 16. Mean human evaluation of complexity as a function of mean fractal dimension estimated from box-counting.

Conclusions

Box-counting dimension appears to be a powerful estimate of an object's complexity, but care must be used in its application. Dimension is not a method for separating objects based on their overall form. Rather, it separates objects based on one aspect of their structure, the relationship between perimeter and scale of observation.

This is not a new finding; McLellan and Endler (1998) compared different methods for measuring and describing the shape of leaf outlines. Fractal dimension was well correlated with the ratio of perimeter to area but was not the best method for differentiating among shapes. In other words, two noticeably different objects can be equally complex and therefore have the same fractal dimension. This is noticeable by looking at the images of *Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Utricularia inflata* (Fig. 10i,j,k). Each of these images is unique and easily discernable, but all were rated as having similar levels of overall complexity (Table 2 and Fig. 12), although the scale specific values of complexity differed (Fig. 14e,f).

The original thought had been that the maximum achieved complexity would correspond to the mean human response. This had resulted from a misapplication of the second axiom of box-counting. While the complexity of the images is strictly relative to the scale of observation, this does not mean that we should attempt to evaluate observations at one particular scale. Rather, the scale of observation covered the entire range of scales from that of a single pixel to the scale where the appearance of the object begins to approach the zero line. Subsequently, people respond to the mean complexity over all these scales, which is a vindication of the third axiom. The probable outcome of the interaction (i.e., perception and evaluation of complexity) was determined to be a continuous averaging function across scale.

How then does this help us to understand the impact of the arena on predator-prey interactions? Consider the variables. We have a surface with a given dimension and complexity. We have a predator, potentially of almost any size, who must travel over and search the arena. And we have the prey, which also must travel the surface of the arena

and can be of almost any size. In more mathematical terms, we have the box-counting function of the arena with two critical points, the scale of the predator and the scale of the prey. Theoretically, any change in predator size, prey size, or arena complexity can affect the overall interaction, but before we develop a mathematical model of their relationships, we need to review what is already in the literature.

CHAPTER 4 REVIEW: PREDATION AND SCALE

Prelude to the Three-Point Interaction

Perception, as examined in the previous chapter, is a two-point interaction. There is an object and a perceiver. Predation as examined here, is a three-point interaction; predator, prey, and arena. Two-point interactions are relatively simple and can be exactly calculated. Three-point interactions introduce the possibility of uncertainty. Insights into the subtleties of the three-point interaction can be glimpsed by trying to understand the various two-way interactions contained within the three-point problem. In this case, the potential two-way interactions are predator-prey, arena-predator, and arena-prey. This chapter reviews the literature on predation that highlights the effect that changing any of the three points has on these two-way interactions.

Predator-Prey Interactions

Parts of Predation

Predation as an act can be broken down into time spent in various activities, each of which can be affected by the other, by change in the sizes of predator and prey, or by changing the complexity of the environment. Searching, pursuit, handling, and digestion all require time investments. Search time is that time spent from when a predator decides to search for food to the time when food is found. For ambush hunters, this is the time spent waiting for prey to come by. Search time is negligible in prey rich habitats but in prey poor habitats it can represent the majority of a predator's time budget. Pursuit is

that time between the detection of a potential prey item and its final capture, or to the point where the pursuit is cancelled in an unsuccessful hunt. Handling time is the time between the capture and final consumption of a prey item. Digestion time is usually the time between final consumption and the decision to start looking for food again. These categories are not strictly exclusive and can show considerable overlap. For instance, animals that inject venom to subdue their prey typically begin an extra-oral digestion at the same time. All of the parts of predation can be affected by changes in the three factors.

Intuitively, smaller prey items will be harder to find and will require more search time than an equivalent number of large prey items. It would seem more symmetrical if increasing predator size had the same impact as decreasing prey size, but increasing the size of the predator reduces the search time. Mittelbach (1981a) found that the number of prey items captured per second of search time increased linearly with a log increase in fish length. The exact relationship depended on the type of prey being hunted, but the general trend of increased feeding rate in response to increased fish length was always highly significant. Mittelbach interprets these results in light of research on the visual ability of fishes. Previous studies have found that the maximum distance from a prey item that will cause a fish to react increases with increased fish size as well as with increased prey length. Interpreted in this light, larger fish have a faster feeding rate because they are able to find more prey. Mittelbach's work provides some support for this in that the fastest feeding rates occurred in the open water experiments where there were no objects to obstruct the fish's field of view. An alternative explanation could allow for the ability of a larger predator to cover the ground faster. Ryer (1988) found

that larger pipefish encountered more amphipods than smaller fish if relatively unobstructed. Not only were their fields of view larger but also larger fish were more likely to attack and more likely to be successful than smaller fish. The implication is that large fish were quicker than small fish. This resulted in larger pipefish having a greater consumption rate per unit body mass, than smaller fish feeding on the same prey.

Changing the relative sizes of predator and prey can dramatically affect handling time as well. The efficiency of an anthocorid predator feeding on aphids increased as the predator to prey size ratio increased (Evans 1976a). A more accurate measure of actual handling time showed that for naiads of a damselfly, *Ischnura elegans* (van der Lind), feeding on a cladoceran, *Daphnia magna* (Straus), handling time decreased linearly with increased damselfly length (Thompson 1975). Similarly, increasing the size of the prey increases the handling time resulting in a maximum size of prey for a given predator. Vince et al. (1976) found that the maximum size of prey eaten by the salt marsh killifish, *Fundulus heteroclitus* (L.), increased with increasing predator size so that growing killifish could consume ever-larger prey items. There is a maximum size for this fish species so that it was possible for prey items to escape predation if they managed to grow big enough. A prey item could also escape predation if it grows faster than its predator. Small instars of the big-eyed bug, *Geocoris punctipes* (Say), could not successfully attack large instar caterpillars of the tobacco budworm, *Heliothis virescens* (F.), but large instar bugs could consume large instar caterpillars (Chiravathanapong and Pitre 1980).

Functional Response

The idea of a predator's attack rate being influenced by the perceived density of prey items is almost the definition of a functional response. Since this dissertation is attempting to determine the relative protection value of plant forms, any changes to

predation rate that incur with increasing prey density are important. A full review of the literature on functional responses is beyond the scope of this report and interested readers are referred to Holling (1961) for an excellent introduction and review of the subject. In general, changes in the relative sizes of predator and prey result in corresponding changes to the attack coefficient and handling times. This has the impact of shifting the functional response to either the left or the right of the prey density gradient. This was well documented by Thompson (1975), who examined naiads of *Ischnura elegans* feeding on *Daphnia magna*. Attack coefficient "a" increased and handling time T_h decreased linearly with increased damselfly length, resulting in a shift in the Holling type 2 functional response.

Nuances of behavior can also influence the functional response. Heimpel and Hugh-Goldstein (1994) examined the functional response of nymphal predatory pentatomids feeding on larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). The pentatomids did not show a typical functional response. At low densities of beetle, predation rate starts out high but then drops as prey densities increase. Predation rate bottoms out and then rises again as prey densities increase. The apparent cause of this pattern is that pentatomid nymphs exhibit area specific searches after a successful kill. At high prey densities, this results in faster location of clumped prey, but at low densities, it merely wastes time. This doesn't explain the initial high success rate at low prey densities. Prey behavior can also impact on the functional response. Tostowaryk (1972) found that the attack rate of pentatomids on sawfly larvae peaked at intermediate prey densities and then declined. This was because the larvae were able to defend themselves more efficiently when in a large aggregate.

The impacts of changes in the arena on the functional response have been less well documented. Occasionally, an arena change can change the type of functional response demonstrated instead of just shifting it. Lipcius and Hines (1986) found that predatory crabs feeding on soft-shelled clams showed a type III response in sand (sigmoid) and a type II response in mud. Topographically similar conditions produced different responses. As previously stated, this was thought to be due to probing action of crabs being hindered by sand. The probing action is a chemosensory searching action, so the impact is on the crabs' perception, and does not affect physical movement or prey capture. The result is increased search times without any change in the handling time.

Handling time does not always impact functional responses. Wiedenmann and O'Neil (1991) compared the functional response of predatory pentatomids in simplified lab settings versus the field situation. The results differed markedly. Lab studies indicated that the pentatomids could attack 14 larvae each per day, but they only achieved 4 or 5 per day in the field. There are different limitations at work here. Search time in a petri dish is essentially zero, so that lab studies highlight the effect of handling time. In the wild, search times are so long that handling time has virtually no effect on the functional response.

Optimal Foraging

Like the functional response, optimal foraging is concerned with predation from the predator's point of view. But while the functional response attempts to numerate how many successful attacks a predator will make on a given prey item, optimal foraging theory attempts to determine how much attention a predator will give to different possible prey items or feeding strategies. Loosely stated, optimal foraging theory speculates that animals feed in a manner that best maximizes food intake while minimizing energy

expenditures. The origins of optimal foraging theory can be traced to a pair of works published sequentially in the same journal. Emlen (1966) and MacArthur and Pianka (1966) presented the idea that animals were adapted to behave in a manner that maximized their net energy gain. The idea that mathematical models could predict feeding decisions made by an animal caught the imagination of scientists and hundreds of papers have since been published on the topic. Numerous subtopics have been developed, but in general, they can be lumped into four categories (Pyke *et al.* 1977); 1) Optimal type of food, 2) Optimal choice of patch, 3) Optimal time spent in a patch, and 4) Optimal movement patterns and speed.

The focus of the present study is the complexity of surfaces and how variously sized predators and prey interact across them. Therefore, the concern here is with what happens to the prey when a predator is already within a patch. Inter-patch decisions can play an important part on the optimal foraging of the predator, but these decisions are dependent on, rather than causative of the small time-scale interactions that are our primary focus. It is for this reason that we restrict our attention to predators and why they feed on particular types of prey, i.e., optimal type of food.

When an animal makes the choice as to which item to eat, we might be able to predict that choice based on the amount of energy "profit" available in that item. Profitability of an item is usually defined as the net food value of an item divided by the handling time needed to consume it. Small handling time thus increases the profitability of a food item by allowing a faster rate of consumption. While it is very straightforward to declare that an animal should always feed on the best item, it becomes a more difficult question to determine how many of the lower quality items to include in the diet. In

general, if animals are presented with a simple choice between food items of different profitability, they will choose the most profitable one (Krebs 1978).

Profitability defined by the relative value of a single individual does not include all aspects of predation costs. Obviously, some time is spent searching and chasing prey items before handling time becomes important. If we define profitability in terms of a rate of net energy intake, we then have a more dynamic measure of a food type's profitability that takes into account its relative frequency. Time spent searching is inversely proportional to the encounter rate, which is a function of the food's density and the speed of the searching animal. Numerous examples of animals feeding optimally have been published in the literature. One of the earlier and best-documented cases involves the bluegill, *Lepomis macrochirus* (Rafinesque), feeding on different sized prey. Werner and Hall (1974) examined the feeding behavior of bluegill in an aquarium, presented with *Daphnia* of three different size classes. If all densities were low, then the encounter rates were also low and the fish made no selection. If all three size classes were presented at high densities, then the fish overwhelmingly preferred the largest class. At intermediate levels the fish chose the two larger size classes and ignored the smallest size class. In other words, if the fish were not being kept busy feeding on the larger size classes, they would take smaller size classes in order to maintain energy flow. They were maximizing the energy intake per unit time. This aquarium study and the model developed to explain it received important validation from a study that examines the growth of bluegill in a natural lake and compared it to the energy intake predicted by the model as well as that predicted by random feeding (Mittelbach 1981a, 1983). The growth

rate of the wild fish correlated with the energy intake predicted by the optimal foraging model but did not correlate with the energy intake predicted by random foraging.

A special note should be made here of the case of ambush predators where the encounter rate is a function of the prey's speed of movement and not the predator's. Here the search time is the sit and wait time. Ambush predators too have been found to feed optimally and a classic example is that of mantids. Charnov (1976) found that mantids fed optimally according to the rational that any food item was optimum if its energy content divided by the handling time was greater than the total available energy of all possible food items divided by the total time spent waiting and handling prey.

Occasionally, a study reveals an animal that is apparently feeding in a sub-optimal manner. For example Goss-Custard (in Krebs 1978) examined the foraging strategy of the redshank, *Tringa totanus* (L.). He found that large polychaete worms were eaten in direct proportion to their own density but that smaller worms were not eaten in proportion to their own density but in inverse proportion to the density of the larger worms. So far this is classic optimal foraging but the redshank preferred a sub-optimal amphipod above any of the worms. It is thought, but not proven, that this apparently bad food choice was a function of mixed currencies. That is to say that while energy was one currency of optimization, there could also have been another currency such as a particular nutrient. The particular feeding pattern observed may not be optimal on energy alone but might represent an optimum mix to maximize the input of both energy and nutrients.

Switching is another phenomenon that can result in an apparently sub-optimal feeding strategy. Switching was coined by Murdoch (1969) and refers to the situation where a predator feeds on a disproportionate number of the commonest prey. If a

different prey becomes the most common, the predator will often switch to specializing on this second prey. Murdoch and Oaten (1975) as well as Murdoch *et al.* (1975) did further work on the topic. A possible explanation for switching is that a predator may become more efficient by specializing all efforts at catching a particular species of prey. Lawton *et al.* (1974) found that *Notonecta* individuals became better at attacking mayfly nymphs as they became experienced. The percentage of attacks that were successful increased with time indicating that experience may improve predator foraging behavior.

Few studies have examined how the structure of the environment affects the optimal foraging of a predator. Indeed, most studies seek to minimize structure in the testing arena in order to examine the decision process in isolation from any habitat effect. While the shape of the environment may not affect the amount of energy represented in a prey item, it can certainly affect almost all other components of optimal foraging models. One of the first studies to investigate the effect of structure on optimal foraging was Mittelbach (1983). In the laboratory experiments, bluegill were placed into aquaria with three different possible structures. The least complicated structure was a plain aquarium filled only with water. The medium complexity structure involved an aquarium with 4-5 cm of marl sediment. The most complex structure involved an aquarium with live, anchored plants. For all three situations, handling time increased exponentially with increasing prey length, but the slope of a log-linear regression increased with increasing complexity of environment, indicating that larger prey were increasingly more difficult to handle in more complex habitats. Not only handling times, but encounter rates were also affected by the complexity of the environment. Lower complexity led to higher encounter rates. This affect was greater for larger fish. This suggests that the encounter

rate was a function of the size of the predator interacting with the complexity. Caution should be used in interpreting this paper. Each of the habitat complexity levels had a different prey species. While length of each type of prey showed the same response, inter-habitat comparisons could be biased, negating the conclusions on complexity. Additionally, complexity was not quantified, so that later papers had to arrive at the values of handling time and encounter rates by experimental analysis rather than measurement (Werner and Mittelbach 1981; Mittelbach 1983).

Prey Size Affected by Predation Technique

While an optimal foraging strategy can definitely determine the size of prey item selected, a change in the manner of predation will also impact size of prey consumed. Schmitt and Coyer (1982) examined the foraging ecology of two sympatric fish in the genus *Embiotoca* (Embiotocidae). Both species are roughly the same size and occur together in temperate marine reefs and both share similar diet. *Embiotoca jacksoni* Agassiz fed primarily on tubicolous amphipods and was able to separate the amphipods from surrounding medium. It fed primarily on small but numerous species and the mean weight of species in its gut contents was not different from that of a random sample of the environment. *Embiotoca lateralis* Agassiz was a more open water feeder and actively hunted the larger and rarer prey species. The mean weight of the individual prey items in its gut was significantly larger than that of *E. lateralis* of the same length.

It is more difficult to show a similar effect within individuals of the same species since the switch between potential prey items is tightly connected with optimal foraging strategies. Murdoch *et al.* (1975) found that guppies, *Poecilia reticulata* Peters, would switch feeding behaviors based on optimal foraging decisions. When the fish were offered either *Drosophila* flies on the water surface or tubificid worms on the aquarium

bottom, they would feed in the manner that offered the greater rewards. In other words, a change in the fish behavior resulted in a prey species bias.

It can also be shown that a particular feeding behavior has an impact on the size frequency of prey items selected. Bluegill take more big prey than small prey. Experiments using *Daphnia magna* as prey items show that the number of a specific size class taken exactly matches that predicted by a model that uses the apparent size (Werner and Hall 1974). Bluegill are visual predators and always feed on the prey item that appears to be larger either because of its size or because of its proximity (O'Brien *et al.* 1976). If large prey is common, then the predators will specialize in feeding on them because the large prey have a greater probability of appearing larger. As large prey becomes less common, small prey items are fed upon with higher frequency since their probability of appearing larger increases. The notion of feeding on prey "as encountered" is affected by the apparent size of an organism.

The technique of feeding on the apparently larger prey item has profound impact on the prey species. Zaret and Kerfoot (1975) noted that predators of a waterflea, *Bosmina longirostris* (OF Muller), primarily used visual hunting techniques. The waterfleas were mostly transparent except for the black pigment of the eye. Ideally, large waterfleas could see food better than small waterfleas, but being large increased their vulnerability to visual predators. Transparency reduced their vulnerability, but to see food requires eye pigment. The result of being visually hunted resulted in large transparent prey with pigment only where it is needed. Presumably, a filter-feeding predator would result in populations of smaller waterfleas with more pigment.

Hunting strategy can interact with prey behavior to have an impact on size selection. Another waterflea species, *B. longispina* (Leydig), reacts to a predator by swarming (Jakobsen and Johnson 1988). The larger waterfleas would move faster into the swarm resulting in smaller waterfleas being near the margins and being disproportionately fed upon by sticklebacks.

Impact of Arena on Predator-Prey Interactions

Price *et al.* (1980) list four different ways in which the plant structure can impact predators. Predators might have different attack rates on different plant species (Haynes and Butcher 1962, Miller 1959, Monteith 1955, Weseloh 1976) or attack rates can vary over different parts of the same plant (Askew 1961, Askew and Ruse 1974, Dowden *et al.* 1950, Evans 1976b, Weseloh 1976). Plants might provide structural refuges for the prey items (Arthur 1962, Ball and Dahlsten 1973, Bridwell 1918, 1920, Graham and Baumhofer 1927, Levin 1973, Mitchell 1977, Pimentel 1961, Porter 1928, Wangberg 1977, Washburn and Cornell 1979) or simply interfere with enemy search movement (Bequaert 1924, Darlington 1975, Ekborn 1977, Hulspas-Jordan and van Lenteren 1978, Katanyukul and Thurston 1973, Levin 1973, Rabb and Bradley 1968, Webster 1975, Woets and van Lenteren 1976).

Changing the relative sizes of predator and prey can dramatically affect handling time. The efficiency of an anthocorid predator feeding on aphids increased as the predator to prey size ratio increased (Evans 1976a). A more accurate measure of actual handling time showed that for naiads of a damselfly, *Ischnura elegans* (van der Lind), feeding on a cladoceran, *Daphnia magna* (Straus), handling time decreased linearly with increased damselfly length (Thompson 1975). Similarly, increasing the size of the prey

increases the handling time resulting in a maximum size of prey for a given predator. Vince et al. (1976) found that the maximum size of prey eaten by the salt marsh killifish, *Fundulus heteroclitus* (L.), increased with increasing predator size so that growing killifish could consume ever-larger prey items. There is a maximum size for this fish species so that it was possible for prey items to escape predation if they managed to grow big enough. A prey item could also escape predation if it grows faster than its predator. Small instars of the big-eyed bug, *Geocoris punctipes* (Say), could not successfully attack large instar caterpillars of the tobacco budworm, *Heliothis virescens* (F.), but large instar bugs could consume large instar caterpillars (Chiravathanapong and Pitre 1980).

Changes in the arena can have dramatic effects on search time. Physically preventing or hindering the movement of predators greatly increases search time. Walking speed of two predators, a coccinellid, *Coleomegilla maculata* (De Geer), and a lacewing, *Chrysopa carnea* Stephens, were seriously reduced on tobacco as compared to cotton (Elsey 1974). This was observed to be due to the glandular trichomes on tobacco hindering movement. A similar phenomenon seems to occur in predatory crabs hunting for soft-shelled clams (Lipcius and Hines 1986). The crabs' success rate rapidly increases with increasing clam density if the crabs are probing in mud. But if they are probing in sand, their success rate is reduced and lags behind increases in clam density. The speculation was that this was due to probing action of crabs being hindered by sand, leading to increased search times.

Since prey density has an effect on search time, changing the size of the arena will impact on the predator success rate. Sometimes this change in density is not immediately obvious. Need and Burbutis (1979) examined the searching efficiency of a parasitic

wasp, *Trichogramma nubilale* Ertle and Davis, searching for eggs of the European corn borer, *Ostrinia nubilalis* (Hubner). In the field, corn leaves gradually expand resulting in more area for the wasps to search. Initially, percentage parasitism increases with time, but eventually there is a point in the season when percentage parasitism begins to steadily drop. In controlled lab experiments, increasing the arena size decreased density of the eggs and as predicted, decreasing the density of eggs decreased the parasitism rate in a linear fashion.

More relevant to the theme being explored here is that it is possible to change the search time by altering the complexity of the arena. Andow and Prokrym (1990) also examined the hunting behavior of *T. nubilale* looking for egg masses of the European corn borer. The hunting surface was a waxed paper onto which egg masses of the European corn borer had been laid. The simple hunting surface was one of these papers folded once and standing on end. A complex surface was one of these papers folded numerous times and standing on end. Parasitism rates were 2.9 times higher on the simple surfaces. With no hosts present, search time was 1.2 times longer on complex surfaces implying an effect on giving up time. Wasps found hosts on simple surfaces 2.4 times faster than on complex ones. Keep in mind that the original pieces of waxed paper had the same dimension. In our terminology, the two papers had the same Euclidean area, but the multiple folded piece of paper had a greater apparent dimension.

While it is normal to think of structural effects on the basis of what their final outcome is, it is more germane to our current discussion to consider the effects on the basis of how they impact predators and prey. To this end, we can divide structural effects into two categories of behavioral and mechanistic effects. Behavioral effects are changes

in the behavior of either the predator or the prey that are caused by changes in structure and mechanistic effects are defined as differences resulting from changes in structure without a change in the behavior of either the predator or prey. Note that these categories are not meant to be mutually exclusive and that combinations can occur.

Behavioral Effects

It is easy to assume that there are more animals in complex areas because the added cover provides a refuge from predation. But we must be careful to separate between the effects of refuge on the differential survival of the prey and some aspect of the structure causing the prey to choose to be in the area. Prey items could be attracted to particular structural characteristics for a variety of reasons. Rejmankova *et al.* (1987) attributed the distribution of larvae of the mosquito *Anopheles albimanus* Wiedemann to oviposition choices made by the adult. They used cluster analysis to define 16 different larval habitats and found that the mosquito was most common in habitats with emergent graminoids. The presence of filamentous algae or small floating plants was detrimental to them. Habitats that were complex on a large scale (e.g., mangrove roots) were not favorable to the larvae.

Most behavioral reactions probably are predator avoidance responses. The avoidance of habitats that were complex on a large scale by adult mosquitoes might be considered an adaptive response considering that these areas are readily accessible by fish. Additionally, the presence of a predator may exaggerate a behavior already present. Lynch and Johnson (1989) found bluegill sought artificial pipes for shelter regardless of predators present or not present, but that a predator being present did result in an increase in the rate of shelter seeking. In this situation, intimidation by predators is visual so it was not surprising that turbid water resulted in less shelter seeking.

It is also not surprising that behavioral responses to changes in complexity have been found to be species specific. Edgar and Robertson (1992) found that when leaves or epiphytes were removed from stems in Australian seagrass beds, some species of mobile epifauna increased and some species decreased. Most species reacted to either the reduction of leaves or epiphytes, but not to both. Decreasing the seagrass density had the same effect on the same species. Cage exclusion in the wild showed that the cause was from active choice and not predator mediated.

Similarly, predators can be attracted to particular structures. It has been argued that areas of greater complexity attract predators because they provide an increased abundance of attachment sites for the associated fauna's food (Abele 1974; Hicks 1980). There is some evidence that this attraction occurs, since mixed vegetable crops attracted and sustained higher populations of predatory anthocorids (Hemiptera) than monocultures (Letourneau 1990). Prey was not the attractant though, since densities of prey items were similar. Cárcamo and Spence (1994) did not measure plant complexity, but they did find that different crops resulted in different predation pressures. They found this to be the result of the ground beetles being differentially attracted to the different crops and not because of any changes in their hunting efficiency.

Aside from choosing to be in areas of particular complexity, predators can change their behavior when presented with differing complexities. Cloarec (1990) found that the presence of the aquatic macrophyte *Hydrilla verticillata* caused belostomatids (Hemiptera) to switch from active hunting to ambush. This effect was independent of hunger level. There was no testing of different density levels and no alternate plant types were tested, but these results do indicate that changes in the amount of structure in the

habitat can change predator behavior. Stoner (1979) had previously found that Pinfish became more selective with increasing macrophyte biomass, resulting in different prey being selected. Different parts of the same plant can cause similar responses. Gardner and Dixon (1985) found that a parasitic wasp searching for aphid hosts on wheat would search each leaf equally, but that the ear of the plant was searched less often. Any aphids on the ear of the plant would be somewhat protected from attack by the presence of the seeds. One explanation was that the wasp was choosing to search areas where aphids had less protection.

Just as in the prey, predator response to change in habitat complexity is also species specific. Frazer and McGregor (1995) used dowels to mimic plant structure and examined the behavior of various coccinellid (Coleoptera) species on these surfaces. They examined movement speeds and the frequency of specific directions of movement. Tendency to move up or tendency to move to the top of an object varied in a species-specific manner. The searching effectiveness of coccinellids would vary between plants as well as between species if these results held for natural plants.

Care must be taken when evaluating behavior in that what appears to be a difference in behavior might in reality be the same behavior operating at a different scale. Price (1983) developed a mathematical model to predict patch choice by "predators". He validated the model with data from seed-eating desert rodents. In other words, the size of the "predator" rodents determined the size of the seed patch that the "predator" would use. Animals of different sizes would appear to be making different behavioral decisions even though they were operating under the same mathematical rules. Lynch and Johnson (1989) found a similar phenomenon. As cited above, they studied shelter seeking by

bluegills in artificial pipes. They found that large fish sought large pipes and that small fish sought small pipes even though they could fit into larger pipes and still receive shelter. Apparently, the fish had some sort of ideal surrounding area to body size ratio that resulted in size selection of refuge.

Mechanistic Effects

Behavior is an important and interesting field of study with many questions yet to be answered, and it does dovetail neatly into our discussion on complexity and predation. However, the central phenomenon in consideration is interaction across a complex surface. Behavior is affected by complex surfaces, but it is generally of interest because it can prevent the interaction. Predator-prey interaction is physical and questions on size, frequency, density, and complexity need to be also considered in mechanistic terms.

Fortunately, there are already many studies published that consider predation in mechanistic terms. These can be divided into two categories. There are those studies that compare changes in the amount of structure. Then there are studies that consider changes in the form of the structure. The concepts of complexity and dimension are contained within both types of study and so both types need to be considered.

Changes in density

Many studies interchange the definitions of complexity as density versus complexity as form. Certainly, the broad definition of complexity, as an object's tendency to occupy space-time, supports the obvious notion that a dense patch of vegetation is more complex than a loose patch. But the two definitions can be measured separately on a box-counting plot. Both concepts are scale specific and interrelated and both concepts can affect the predator-prey interaction. There have been a number of studies on each meaning of complexity, but sweeping generalities have proven to be

elusive. It has proven to be easier to draw conclusion about density since density is easier to measure than dimension.

The simplest experiments on the impact of density compare the feeding efficiencies of predators in empty versus heavily planted arenas. The most commonly reported phenomenon is that the presence of structure does not alter the fundamental dynamics but rather draws them out over time and merely delays the final outcome. This has been found to be true for European perch, *Perca fluviatilis* L., which quickly eliminated large predatory invertebrates from areas lacking vegetation, but needed more time to have the same impact in vegetated areas (Diehl 1992). The impact is thought to represent a slowing down of the predator either by increasing the amount of area it would need to search or by physically impeding its movements. Luckinbill (1973) demonstrated this with laboratory populations of *Paramecium aurelia* Ehrenberg and its predator *Didinium nasutum* OF Muller kept in culture. Without structure, the situation was unstable. Populations would fluctuate in cycles of increasing amplitude until one or the other of the predator and prey went extinct. Structure was added in the form of methylcellulose, which slowed the frequency of contact but offered no preferential degree of movement to either species. The fundamental dynamics did not change, but were prolonged over time. Sometimes, this prolongation may be enough to allow for the survival of a prey species. Russ (1980) increased density of structure by placing models of arborescent bryozoans on a coral reef. Fish foraging efficiency was reduced and the survival of colonial ascidians was enhanced.

A problem with the all or no vegetation experiments is that we cannot note the effects of intermediate levels of structure in the environment. Most studies have found

predators show a step function response to increasing plant density (Nelson 1979; and Heck and Orth 1980). That is, the fish in these studies showed little response to increasing plant densities until a threshold level had been reached. At this point, there was a sudden dramatic decrease in predator success rate that was only slightly worsened by further increases in plant density. Savino and Stein (1982) found this same step function response to increasing plant stem density with largemouth bass, *Micropterus salmoides* (Lacepède), attacking bluegill in artificial pools. The decline in predation success with increasing plant density was thought to be due to an interaction between the predator's visual range being blocked and changes in the behavior of the prey. This idea of plant density hindering the predator's visual tracking of the prey was supported by Minello and Zimmerman (1983). They mimicked the structure of reeds by using drinking straws, and examined three different densities of straws on the predation success of four different fish species. Two fish species were negatively affected while two others were not. In general, mode of predation did not matter, but predatory efficiency did. Inefficient predators were most affected. The authors believed that this was related to the predators' need to reacquire their targets after an initial strike failed. Predators that were usually successful on the first strike were little affected.

Care must be taken when trying to extrapolate these confined experiments to natural situations. Natural areas are open systems where both predators and prey may enter or leave when they wish. Sometimes the closed system results are repeated in a more open naturalistic setting. Bettoli *et al.* (1992) examined the feeding behavior of largemouth bass in a reservoir with 39-44% coverage by macrophytes. In such a situation, the largemouth bass did not usually feed on fish until the young largemouth

bass were at least 140 mm total length. When the vegetation was removed with grass carp, *Ctenopharyngodon idella* (Valenciennes), largemouth bass as small as 60 mm total body length consumed fish. This led to faster growth of the largemouth bass when macrophytes were absent. There was no difference in forage fish densities, so vegetation did seem to reduce the feeding efficiency of the young largemouth bass.

At other times, the natural system seems to defy the predicted outcomes from small closed aquaria. Savino *et al.* (1992) found that altered plant densities in the wild caused no change in bluegill diet and growth. In the wild, higher plant densities supported higher invertebrate densities. It is possible that invertebrate densities became high enough to overcome any refuge effect. In other words, the probability of any given invertebrate being eaten was lower in high plant densities but there were so many invertebrates there that the fish had no trouble finding enough to eat.

Even in closed systems, the presence of structure has been found to occasionally increase a predator's success rate. Stoner (1982) found that large pinfish consumed more amphipods in low biomass experimental tanks than in bare sand aquaria. One way that this could be explained is if there were two opposing functions in operation. This is thought to be the case in an experiment conducted by Mullin *et al.* (1998) in which gray rat snakes, *Elaphe obsoleta spiloides* Duméril, Bibron and Duméril, were allowed to forage in enclosures with varying levels of structure added. Snakes were most successful at capturing prey when searching in enclosures with a moderate level of structure. They were less successful in barren cages and in cages with highly complex structures. The explanation was put forward that the snakes benefited from seeing their prey (low

structure) but also benefited from hiding from their prey (high structure), so that optimal hunting success occurred at medium structure levels.

In other situations, success rates in moderately dense environments may seem to be higher because the low-density environment, which truly had a higher rate, was rapidly depopulated. Crowder and Cooper (1982) found that bluegill introduced into ponds of low plant density rapidly depopulated many invertebrate species resulting in only the few surviving species forming the long-term diet. At higher plant densities, the fish concentrated on large, easier to find invertebrates, while at intermediate plant densities, the fish ate more species and grew better.

The effect of plant density on predation becomes even more difficult to generalize when we allow for species behavioral changes. A given predator may hunt in one manner at low densities and potentially in a completely different manner at high densities. Anderson (1984) showed that the hunting technique of largemouth bass changed depending on the density of plants in the aquarium. Fish were presented with either guppies or damselfly larvae. When hunting for guppies, fish swam rapidly and scanned quickly. When hunting for damselflies, fish swam slower and searched more diligently. In a sparsely planted aquarium, the fish ate all the guppies first. In a heavily planted aquarium, searching speed for guppies dropped and the encounter rate dropped even faster. Searching speed for damselfly also dropped but the encounter rate dropped proportionately. In this situation, the fish ate a couple of guppies then began searching for damselflies, eating prey as they came across them.

Not only do predators change their behavior in response to changes in prey species and plant density, but also different species of predator react in different ways. In

addition, each prey species changes behavior in a specific manner dependant not only on plant density but also the hunting style of potential predators. Savino and Stein (1989) examined the effect increasing plant density had on the predatory actions of largemouth bass and northern pike, *Esox lucius* (L.). The success rate of the largemouth bass was negatively impacted and their hunting tactic switched from searching to ambush. The northern pike were relatively little impacted possibly because they were ambush hunters regardless of plant density. While increasing plant density did reduce predation the effect on a specific prey type was determined by the species reaction to predators. Fathead minnows, *Pimephales promelas* (Cope), showed almost no behavioral changes to changes in predator species or plant density. Although somewhat protected by increased plant densities they were still vulnerable at all densities. Bluegill were more closely orientated to the actions of the predator. If a searching largemouth bass was following them, they were more likely to be shoaling. If a northern pike was in the tank with them, then shoaling offered little protection and the bluegill were more dispersed. They reacted to an attack faster than the fathead minnows and sought out structure to hide behind. This resulted in bluegill suffering little predation at the highest plant densities.

While occasionally complicated, predator and prey responses to increased plant density are inherently understandable and fairly predictable once the variables are known. But every now and then, a study is published that suggests that something other than density is affecting the results. Marinelli and Coull (1987) published one such study. They examined the effect of polychaete worm tubes on the predatory interaction between juvenile spot, *Leiostomus xanthurus* Lacépède, and the benthic meiofauna from the nearby marine habitat. The tube structures were mimicked using plastic drinking straws

of varying density. Fish caused significant reductions in four out of six meiofaunal categories. As in some of the previously mentioned studies, they noted that adding some structure resulted in more meiofauna being eaten. Something about the tubes facilitated the predators, but only for certain taxa of prey. There was a notable difference between meiofauna and macrofauna, a phenomenon that has been reported before (Woodin 1978,1981; Bell and Woodin 1984). The implication is that refuges affect various size classes of benthos differentially. While density can be considered in a scale-specific manner and it undoubtedly has an impact on predator success rates, the concept of size-specific changes in measured responses fall more neatly into our concept of complexity as dimension. In other words, form matters.

Changes in form

If form matters, then one should be able to demonstrate that predator-prey interactions vary in a manner that is dependent on the arena. The literature is full of examples of a predator's success rate being dependant on the plant or other substrate type. But to show that the physical complexity of the arena, as measured by apparent dimension, is influencing the relationship, then one needs to demonstrate size-specific and size-consistent responses across a variety of substrate complexities. No previously published paper has yet nailed down this distinction but some of them come close and definitely lend support to the idea of apparent dimension impacting the predator-prey interaction.

The simplest of these studies considers the same suite of predators and prey but compares them in different types of habitat. Russell (1989) found that predation rates were higher and prey survival lower in agricultural areas with two or three crops growing simultaneously as compared to monocultures. Although we are given no idea about the

complexity of the plants, the point is made that a change in plants led to a change in predation rates. Russo (1987) performed a more controlled experiment in which he examined the effect of increasing habitat complexity on the predation of the gray damselfish, *Abudefduf sordidus* (Forsskal), on ephiphytal amphipods. Artificial habitats consisted of aquaria variously "planted" with black nylon bottle brushes. Using brushes of slightly different shape varied complexity, which was measured as the ratio of brush surface area to volume. He did find that increasing complexity led to increased survival of the amphipods but he failed to control for mass of the brushes. Instead of putting equal volumes of brushes into each tank, he put in equal numbers of brushes. As the more complex brushes were also bigger, it cannot be determined whether the increased survival of the amphipods was due to increased habitat complexity or increased habitat density.

Orr and Resh (1989, 1991) published a more definitive pair of studies. They examined the survival of mosquito larvae (*Anopheles* sp.) being raised under four cover types with predators either present or absent. The cover types were parrotfeather, *Myriophyllum aquaticum* (Vell.)Verde, water smartweed, *Polygonum coccineum* Muhlenb., fennel pondweed, *Potamogeton pectinatus* L., and open water. The predator used in these experiments was the western mosquitofish, *Gambusia affinis* (Baird and Girard). When *G. affinis* was present, parrotfeather provided the mosquito larvae with better protection than fennel pondweed (18 vs. 14% survival). Water smartweed and open water had nearly 100% mortality with *G. affinis* present. Using a below water intersection method as well as above water biomass estimates, the authors were able to rank these plants from most complex to simplest; parrotfeather > water smartweed >

fennel pondweed > open water. This matched the experimental survival as well as field densities of *Anopheles* larvae.

What these studies seem to suggest is that increased complexity of the environment offers more protection to potential prey items. Such a simplistic interpretation does not allow for the many nuances of predator-prey interaction. Under this paradigm we would be hard pressed to explain why one size class of prey is eliminated while another is provided protection. Neither does it explain why the presence of cover allows some predators to achieve greater success than they would in the absence of cover. But what we can hold in our mind from these types of studies is that the probability of surviving a predator is dependent on the surroundings and that form of the arena appears to play a role.

We obtain more insight into that role when we examine studies that considered the survival of a single prey type across different habitat types when the size class or species of predator was made to vary. Grevstad and Klepetka (1992) examined the foraging behavior of four different species of coccinellid beetles feeding on cabbage aphids on different varieties of plants. The plant variety significantly affected predation rates. In this case, the effect came from differences in the beetles' ability to traverse the plant. Slippery leaves were difficult to cross so that the beetles tended to stay near the edges. Increased complexity led to the beetles being better able to cover the whole area. Increasing complexity too much led to increases in prey refugia and a decreased predation rate. There were differences in each beetle species' abilities, but they did not vary much in size. In essence, this study really had only one size class of predator. Dean and Connell (1987c) conducted a study in which three sizes of kelp crab, *Pugettia*

producta (Randall), were allowed to forage over two species of algae. Each of which was tested at two levels of algal surface area. The single most significant result was that the larger the crab, the more invertebrates it ate. This is of course, the same result as measured in our predicting the obvious experiment. More interesting, they found that higher surface areas of algae reduced the rate of predation. They found that there was no consistent difference between algae species in the degree of protection provided by a given surface area, but the 3-way ANOVA showed a significant interaction between crab size, algae species, and algae surface area. The point to consider here is that the rate of predation changed with changes in crab size and with changes in surface area, but how fast those changes occurred could not be predicted by measuring the surface area of a particular species of algae. One explanation is that the different sized crabs encountered differences in the algae not measured at the scale where the surface areas were measured.

Further insight is gained from studies in which a single type of predator is allowed to prey upon multiple size classes of prey items across varied habitats. Stein (1977) examined the feeding response of largemouth bass feeding on northern clearwater crayfish, *Orconectes propinquus* (Girard). The largemouth bass would preferentially take the smaller crayfish first and then work their way up the size gradient. If the crayfish were presented on sand, this is exactly what happens. If presented on pebbles, then the largemouth bass choose intermediate sized prey first and then work their way up. If presented on large substrates, then the largemouth bass take the largest prey first. Northern clearwater crayfish are spiny and aggressive and require a lot of handling. Supposedly, the largemouth bass were feeding in an optimal manner that balanced the cost of the meal with its abundance. As the habitat complexity changed, handling costs

would remain constant. So any change in the largemouth bass' diet must have been reflective of the largemouth bass' ability to find the prey items. Note that the size of the objects making up the substrate seems to represent the dividing line. All northern clearwater crayfish over the size of the substrate are taken in order of smallest to largest, but all northern clearwater crayfish under the size of the substrate are taken in the order of their probability of being found (largest to smallest).

Similar results were found for birds. Kelly (1996) examined the prey preference of wild populations of belted kingfishers, *Ceryle alcyon* (L.). Water-filled plastic tubs were set out as feeding stations and the substrate was sand, gravel, or cobble. In simple habitats (sand) the birds preferred larger fish (11-13 cm long) to smaller fish or crayfish. As habitat complexity was increased (sand → gravel → cobble), the birds' prey selections began to mirror a random selection of prey availability.

Iribarne (1996) presented an interesting study that showed size specific vulnerability to a predator, that varied depending on habitat. An amphipod species, which lives in oyster shell habitats, is preyed upon by juvenile dungeness crabs, *Cancer magister* (Dana). Increasing the depth of the oyster shell layer led to increases in the amphipod population. Field experiments revealed that amphipod populations were lower when the shells were whole and higher when they were fragmented. Abundance of dungeness crabs was unaffected by shell depth or fragmentation. This suggests the amphipod population response is derived from a refuge from predation. Laboratory studies showed that fragmentation had little to no effect on predation of single amphipods, but when the amphipods were in copula, they suffered much higher predation among the whole shells than among fragmented ones. In this study we see that predation

on two size classes of prey, single and *in copula*, varies independently across two levels of habitat complexity. While changing the habitat has little impact on single amphipods, there is a dramatic effect on mated pairs of amphipods. The implication is that crushing the oyster shells did not change the habitat much at the smaller scale but changed it dramatically at the larger scale.

The impact of inanimate substrate certainly seems to elicit a size specific response in predation rates but few studies have considered plant form as a substrate. Coen *et al.* (1981) examined the effect that plastic plant shapes had on pinfish feeding on two shrimp species. Plastic *Vallisneria* cut predation in half, while a more complicated plastic red algae form cut it to one quarter. Dionne and Folt (1991) examined the effect of plant form on a predator searching for different prey types. The model predator was the pumpkinseed sunfish, *Lepomis gibbosus* (L.), and its prey items were a species of Cladocera, *Sida crystalline* (OF Muller), and a larval Coenagrionidae. Fish were placed singly into small aquaria planted with *Potamogeton amplifolius* Tuckerman, a thin stemmed and broad-leafed plant, or *Scirpus validus* Vahl, a thick stemmed and leafless plant. Two densities were examined, slightly below the lowest measured field density to approximately two thirds of the highest measured field density. This represented about a twofold increase in density and had no effect on capture rates of either prey species. Plant form however, had a dramatic effect. Capture rates of *S. crystalline* in *P. amplifolius* were 53% lower than in *S. validus*. More dramatically, capture rates of Coenagrionidae in *P. amplifolius* were 365% lower than they were in *S. validus*. It was speculated that the smooth, simple *S. validus* provided less hiding places than the more complex *P. amplifolius*. They suggested that *S. crystalline* had less overall change

because they were more cryptic than the Coenagrionidae on either plant. They did measure the average body length of both prey species, 1.81 mm for *S. crystalline* and 11.58 mm for Coenagrionidae, but made little mention of this as a possible explanation for differences in the predation rates.

Summary

Predation is a complex process involving a series of behaviors each of which can be influenced by changes in the size of predator or prey or by changes in the complexity of the environment. Searching, pursuit, handling, and digestion are all affected by the relative sizes of predator and prey but the interaction with arena complexity is usually less obvious. At a given prey density, smaller prey items require the predator to spend more time searching for them, but the larger the predators, the faster its ability to search. Small prey can remain hidden but are otherwise helpless against a predator. Bigger prey items are more easily found but are not easily taken by small predators. In addition, if a predator wishes to increase the food intake rate, it must choose between big prey and numerous prey. All of these relationships become more complicated when the arena is varied.

Functional response as a broad-scale pattern of feeding dynamics has proven to be sensitive to changes in arena but not necessarily in a predictable manner. Specifically, the interactions between searching time and handling time vary not only with prey density but also with arena structure. In some situations, changes in arena structure will change the apparent density of the prey. This has an inevitable effect on which prey item a choosy predator will take, resulting in seemingly sub-optimal foraging. In other

cases, the predator may change its entire technique dependent on the relationship between prey size-frequency and habitat structure.

If we try to examine just the impact of arena on the predator-prey relationship we run into the problem of separating out behavioral adaptations to the interaction from the actual impact of arena. While potentially complicated, behavioral adaptations are readily understood. But rather than being understandable in the sense of finding some universal adaptations, behavior tends to be species specific. In one sense, behavior can be thought of as a particular species strategy for removing itself from the broad generalities of predation.

Mechanistic effects are the broad generalities of predation. While there are numerous adaptations for dealing with them, density and form of structure in the environment are at the root of the predator-prey interaction. Visibility and accessibility of potential prey items are directly related to the complexity of the surrounding structure and in turn impact everything that has been discussed in this section. Yet, studies on the impact of structural complexity have been inconsistently defined. Some studies concentrated on density, others on form, and others still compounded the two. Small wonder that they sometimes produced contradictory findings.

Box-counting proved to be a powerful tool in predicting the human response to the complexity of an image. Perhaps it could also be useful in quantifying the structural complexity of the environment. An objective measure of habitat complexity would allow us to predict the predation pressure on a given prey species and could prove tremendously useful in our understanding of why animal communities exist in the size and frequency that they do. But is the human perception of complexity directly comparable to the

complexity of the arena as it impacts on predator and prey? In other words, can we use box-counting to determine the relationship between predation and structure? The next chapter presents a series of experiments designed to answer this question.

CHAPTER 5

PREDATION ON A COMPLEX SURFACE

Without a doubt, the physical structure of the arena has an impact on the success of predators and the survivability of prey items. Kareiva and Sahakian (1990) showed that plant structure impacted herbivore survivability only in the presence of a predator. Aphids were placed onto two varieties of pea plants, one with and one without leaves. There was no significant difference in aphid population growth on the two varieties (<10% decline), but if ladybird beetles were added, growth rate on the leafless peas was <50% of that on the normal peas.

In my opinion, Stoner (1979) wrote the definitive statement on the importance of physical structure on the predator-prey relationship and I can do no better than to quote the following passage directly:

"...food webs and predator-prey relationships are not static systems. Variation in habitat structure over space and time may dramatically alter not only the behavior of the predator, but undoubtedly influences patterns of abundance and species richness in both prey and predator groups. The physical structure of the habitat is, therefore, inextricably related to the population and community dynamics of its inhabitants."

In their landmark review, Price *et al.* (1980) argued that predators on a plant represented part of a plant's battery of defenses against herbivores. They provided extensive references on chemical aspects of a plant that affect the predators but gave no consideration to the structural aspects that hindered the predators. If the structure of the plant is an important force in the interaction between predator and prey then how could

box-counting be utilized to help us quantify this impact? Let us break down the behavioral aspects of predation and consider the consequences of a non-linear arena. Searching involves scanning the immediate surroundings and trying to pick out the potential prey items. If we assume that human searching ability is an adequate model for the searching ability of any given predator, we can say that the predator is potentially searching at any of the scales it is physically capable of. It may be quickly scanning the arena at a low resolution (i.e. searching for large scale objects) or it may be picking through the arena at a fine level of detail. If we assume that the predator recognizes the prey item right away, then at any given instant of time, the probability of detecting a prey item h by random searching would be proportional to the size of h at scale s divided by the size of the arena at size s . Keep in mind that detecting an object is the equivalent of striking it with a line of sight. More specifically, the probability of striking an object is proportional to its mean visual angle (2).

However, given that the predator and prey can be anywhere within the arena, then the probability of striking a particular prey item with a line of sight should be proportional to the mean width of that prey item (w_i) divided by the sum of the mean widths of all objects in that arena.

$$P(x_i) = \frac{w_i}{\sum_{e=1}^n w_e}$$

Mandelbrot (1983), in chapter 12 of his book, developed the techniques for comparison of the length, area, and volume of fractal objects. Loosely stated, these measures have a constant relationship to each other dependent entirely on the class of object being compared. For instance, squares have the following relationship.

$$L = 4a^{1/2}$$

and circles have the following relationship.

$$L = 2\pi^{1/2} a^{1/2}$$

Fractal objects hold a similar relationship except that length is a function of scale (s) and dimension (D_f) so that for any object measured at a particular scale, the following holds true (Mandelbrot 1983).

$$L^{1/D_f} = ka^{1/2}$$

with k being some constant dependent on the class of objects. If the prey and the structure making up the arena are considered as specific classes of objects, this relationship should hold. If class of object is kept constant, then perimeter length and area are related as above. This results in recognizably similar forms regardless of size of the objects.

This relationship can be extended to accommodate our interests. Mean width of an object (w) is also a constant function of the root of the area so that mean width is also a constant function of perimeter length.

$$w = za^{1/2}$$

$$\frac{L^{1/D_f}}{k} = \frac{w}{z}$$

$$L^{1/D_f} = \frac{k}{z} w = Cw$$

where C is a constant composed of the two constants k and z. This implies that at any particular scale, the probability of striking a particular prey item with a line of sight should be proportional to the actual measured perimeter length of that prey item ($L(i)$) divided by the sum of the lengths of all objects (n) in that arena all measured at scale s.

$$P(x_i|s) = \frac{L(i)}{\sum_{e=1}^n L(e)}$$

Now suppose we wish to compare two different classes of object, say the probability of a predator randomly noticing a prey item (h) in and around a plant (a) in the arena. The formula for probability based on mean width should still hold but if the size of the prey item is small relative to the size of the plant, dividing the width of the prey by the width of the plant can approximate the probability.

$$P(x_h) = \frac{w_h}{w_h + w_a} \approx \frac{w_h}{w_a}$$

Since the prey and the plant are different classes of objects, each has a different constant involved in computing perimeter length from mean width.

$$\frac{C_h w_h}{C_a w_a} = C' \frac{L(h_s)}{L(a_s)}$$

so that

$$P(x_h|s) \approx C' \frac{L(h_s)}{L(a_s)}$$

This means that the relative probability of detection between two prey items is proportional to their relative sizes and that the relative probability of detection for the same prey item in two different arenas is proportional to the relative sizes of the arenas. Note that as long as all predators process information at the same rate, the probability of detection is independent of predator size. If all scales of observation are equally likely, then the overall probability of detection is proportional to the mean probability of detection ($P(x_h)$) over all scales. However, predators learn to hunt at particular scales or are born with the ability. So, the probability of s occurring ($P(s)$) must be factored in.

$$P(x_s) \approx kP(s) \left(\frac{L(h_s)}{L(a_s)} \right)$$

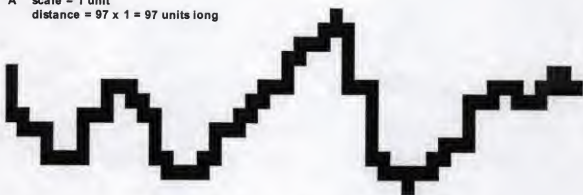
The total probability of detection of a given individual h , would therefore be the integration of this function over all of s .

$$P(X_h) \approx k \int_{-\infty}^{\infty} P(s) \left(\frac{L(h_s)}{L(a_s)} \right) ds$$

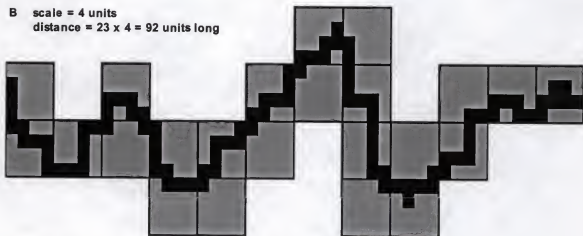
We must also account for pursuit as a component of predation apart from searching. Even if detected, a given prey item may be immune to predation because the portion of the arena it occupies is inaccessible to the predator. Details of the arena smaller than the prey item or larger than the predator would not hinder the predator, but any aspects of the arena larger than the prey and smaller than the predator could interfere. The refuge offered in this manner need not be absolute. Structural complexity at these scales might offer a relative refuge to a given individual if it were easier to access some other prey item. A possible way to quantify this refuge using box-counting would be to create a refuge index (r). If we take the size of the arena measured at the scale of the predator ($L(a_p)$) and subtract it from the size of the arena measured at the scale of the prey ($L(a_h)$), we have an estimate of the amount of space available to the prey that is not available to the predator. The probability that the prey is in inaccessible space would then be proportional to this difference divided by the total area available to the prey multiplied by some constant. The probability that the prey is accessible is proportional to 1 minus this value. This formula is presented below and a stylized rendition of this relationship is shown in Figures 17 and 18.

$$P(Y_h) \propto 1 - r = 1 - \left(\frac{L(a_h) - L(a_p)}{L(a_h)} \right) = \frac{L(a_p)}{L(a_h)}$$

A scale = 1 unit
distance = $97 \times 1 = 97$ units long



B scale = 4 units
distance = $23 \times 4 = 92$ units long



C scale = 8 units
distance = $9 \times 8 = 72$ units long

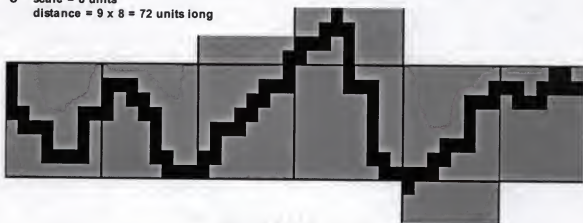


Figure 17. Stylized image of Richardson effect on a hypothetical surface as measured by box-counting. A) Estimated length at scale = 1 unit. B) Estimated length at scale = 4 units. C) Estimated length at scale = 8 units.

A 96 spaces

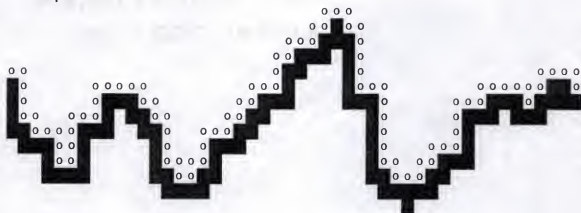
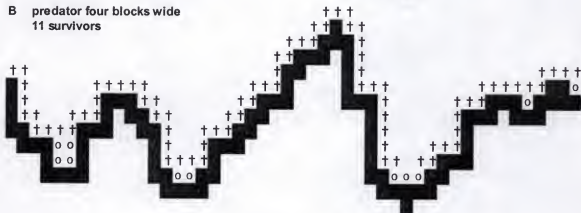
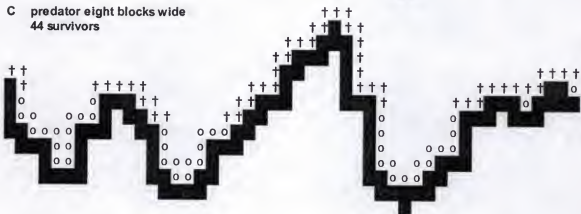
B predator four blocks wide
11 survivorsC predator eight blocks wide
44 survivors

Figure 18. Mortality (†) of prey items (o) on a complex surface after being attacked by a predator. A) Total available room for prey. B) Predator four blocks wide. C) Predator eight blocks wide.

While being totally hypothetical, Figures 17 and 18 show how the concept of accessibility works. Figure 17 illustrates the now familiar phenomenon of apparent length of a complex surface being relative to the scale of measurement. In other words a predator viewing this object "sees" a length relative to his scale. Accessibility of prey items one unit wide would be determinable for predators 4 and 8 units wide as follows.

$$P(Y_h|p=4) \propto \frac{L(a_p)}{L(a_h)} = \frac{92}{97} \approx 0.948$$

and

$$P(Y_h|p=8) \propto \frac{L(a_p)}{L(a_h)} = \frac{72}{97} \approx 0.742$$

while Figure 18 shows that the total mortality of 1 unit wide prey items were 88.5% and 54.2% from predators 4 and 8 units wide, respectively. This is not to imply that this exact relationship will hold for all cases, just that the probability of prey being accessible will be function of $1-r$. The probability of any particular prey item h , being preyed upon ($P(Z_h)$) should be the probability of X_h and Y_h occurring together.

$$P(Z_h) \approx P(X_h) * P(Y_h)$$

If we are intent on measuring how many individuals of the prey species will survive a predator, then we need to determine the probability of detecting one of n_i individuals.

$$P(x_s) \approx kP(s) \left(\frac{n_i L(h_s)}{L(a_s)} \right)$$

If the number and/or size of the prey items begin to be a significant portion of the arena then the following formula would be more accurate.

$$P(x_s) \approx kP(s) \left(\frac{n_i L(h_s)}{L(a_s) + n_i L(h_s)} \right)$$

And the overall probability of detection will be as follows.

$$P(X_h) \approx k \int_{-\infty}^{\infty} P(s) \left(\frac{n_i L(h_s)}{L(a_s) + n_i L(h_s)} \right) ds$$

Note that a small margin of error was introduced because the constants for converting w_i to L_i were not the same for prey as for plants. The error should be minor if the constants are close or if the total length of all prey items is still fairly small.

In the absence of any behavioral traits, the probability of a given prey item being accessible is unaffected by the number of other prey items in the arena so that $P(Y_h)$ is unchanged and the overall probability of predation should follow the following formula.

$$P(Z_h) \propto \left(k \int_{-\infty}^{\infty} P(s) \left(\frac{n_i L(h_s)}{L(a_s) + n_i L(h_s)} \right) ds \right) \cdot \left(\frac{L(a_p)}{L(a_h)} \right)$$

This onerous looking formula can be summarized by saying that the probability of a given prey item being eaten is a function of its probability of being detected multiplied by the probability it is accessible to the predator once detected. Testing these theoretical conclusions requires an experimental setup where it is possible to change the sizes of the predator and prey in arenas with different complexities, without introducing confounding factors. The next three sections detail the experiments that tested these conclusions.

Predicting the Obvious

Introduction

A predator feeds at a given rate based on numerous factors such as body mass, level of hunger, metabolic rate, etc. If all potential variables are kept relatively equal,

then the ingestion rate of an animal (I) has been determined to have a power law relationship to the mass of the animal (Peters 1983) that follows one of the following formulae.

For homeotherms

$$I = 10.7W^{0.703}$$

For poikilotherms

$$I = 0.78W^{0.82}$$

where I is expressed in Watts and W is the body mass of the animal in kg. If we assume prey items are composed of a constant amount of energy (Watts) per unit body mass, then I can also be expressed as a rate of biomass consumption. Additionally, there is well-documented evidence that any linear measurement of an animal will have a power law relationship to the mass of the animal. Given this, it should be possible to find a relationship between the biomass of animals eaten (M) and the body length of the predator ($L(p)$) that will agree with the following format (Peters 1983).

$$M = \lambda L(p)^e$$

This relationship could be expressed as the number of individuals preyed upon (n_p) by dividing M by the mean mass of an individual prey item (m_i).

$$n_p m_i = M = \lambda L(p)^e$$

$$n_{pi} = \frac{M}{m_i} = \frac{\lambda L(p)^e}{m_i}$$

For the larger purpose of this work, we are interested in determining how the plant surface interferes with M . To this end, different size classes of predators will be presented with different size classes of prey in arena altered by including plant material

of different levels of complexity. However, before we can determine the effect of plant material on M , we need to determine what the default levels of λ and e are for a particular arena. So this experiment will test the obvious notion that larger predators will eat more of a given size class of prey than will a small predator. More importantly, this experiment will help to determine the exact relationship between M and $L(p)$, which will lay the groundwork for manipulating the arena and teasing out the finer relationships between predator, prey, and arena complexity.

Materials and Methods

The decision was made to experiment with aquatic animals because of prior familiarity and because it is easy to isolate aquatic animals in small containers that are readily accessible to manipulation. The eastern mosquitofish, *Gambusia holbrooki* (Hildebrand), was chosen as the model predator. Some authors consider it a subspecies of *G. affinis* with a broad range of interbreeding, but since our specimens key out clearly as *G. holbrooki* (Etnier and Starnes 1993), we will consider them as separate species. The eastern mosquitofish is a live-bearing topminnow from the family Poeciliidae and is native to the southeastern United States. It is an adventitious feeder, known to prey readily on insects, crustacea, zooplankton, and algae and has been shown to be more concerned with prey availability than with food choice (Meisch 1985). It is a continuous breeder so that fish of all possible size classes are readily available. Fish were collected from experimental ponds at The University of Florida, Center for Aquatic and Invasive Plants. They were maintained in 38-liter aquaria and acclimated to dry food and captive conditions. Sick or crippled fish were eliminated from the study. Wild caught fish

adapted readily to aquarium life. They began feeding on flake food within one day and learned to associate humans with food within one week.

Larvae of the yellow fever mosquito, *Aedes aegypti* (L.), were chosen to be the model prey. This container-breeding mosquito is tolerant of a wide range of water conditions and is easily cultured in the lab. Its eggs can be dried and stored for long periods of time and triggered to hatch by immersion in water. Eggs were obtained from a long-term culture maintained at The University of Florida, Department of Entomology & Nematology, Medical Veterinary unit. Larvae were hatched and reared at room temperature in untreated well water obtained on site. Eggs were placed overnight in a beaker for hatching. The next morning, first instar larvae were transferred to shallow plastic tubs filled to a depth of about 5 cm. The larvae were fed powdered commercial flake food upon initial transfer and again three days later.

The experimental arenas were 4-liter glass battery jars filled with 3 liters of well water from the same source as used to maintain the fish and rear the mosquitoes. The jars were allowed to sit for 24 hours prior to experimentation in order for the water to degas and reach room temperature of 78° F (25.6° C). Fish to be used in the experiment were deliberately selected to represent a wide range of body lengths and were transferred to a previously unused aquarium where they were starved for two days prior to experimentation. On the day of an experimental run, 200 fourth instar mosquito larvae were hand dipped out of the rearing containers and placed into each of 24 jars. The larvae were allowed to settle down for approximately one hour. Preliminary trials had indicated 200 fourth instar larvae to be near the upper limit of consumption for large *G. holbrooki*. One fish was then placed into each jar. The fish proved to be highly excitable

and some would react with violent panic to casual passers by. The entire area was thus surrounded by a drape of black plastic. This prevented the fish from seeing room activities and resulted in a calming effect. After 24 hours, the fish were removed and their maximum total body length measured. Fish ranged from a low of 15 mm to a maximum of 45 mm maximum total body length. This information was recorded along with the number of surviving larvae. It was assumed that the fish ate the number of missing larvae. Two experimental trials were performed for a total of 48 jars and 9,600 mosquito larvae.

Results

This is a relatively simple experiment involving one experimental variable, fish size. The response variable is number of mosquito larvae eaten. The results of this experiment are presented in Figure 19. Simple linear regression showed a positive significant relationship ($p < 10^{-6}$) between number of mosquitoes eaten and fish maximum total body length (Table 3).

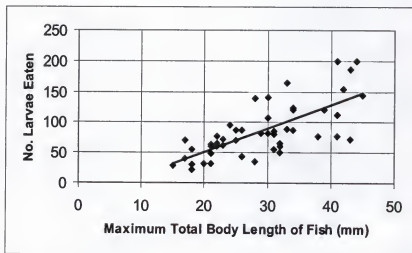


Figure 19. Number of fourth instar mosquito larvae, *Aedes aegypti*, eaten by fish, *Gambusia holbrooki*, over a 24-hour period. ($y = 3.85x - 25.84$, $R^2 = 0.52$)

Table 3. ANOVA analysis on the effect of maximum total body length of *Gambusia holbrooki* on the number of fourth instar *Aedes aegypti* larvae consumed over 24 hours.

<i>Regression Statistics</i>					
Multiple R	0.72				
R Square	0.52				
Adjusted R Square	0.51				
Standard Error	31.52				
Observations	47.00				

ANOVA					
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Significance F</i>
Regression	1.00	49359.12	49359.12	49.69	8.63×10^{-09}
Residual	45.00	44704.71	993.44		
Total	46.00	94063.83			

	<i>Coefficients</i>	<i>Stand. Error</i>	<i>t Stat</i>	<i>P-value</i>
Intercept	-25.84	16.74	-1.66	0.10
	3.85	0.55	7.05	8.63×10^{-09}

<i>Lower 95%</i>	<i>Upper 95%</i>
-61.47	5.96
2.78	5.00

This is an obvious relationship, but one that contains great variability. The formula for the best straight line (Fig. 19) has an R^2 value of only 0.52. So the formula poorly predicts fish predation with there being too much inter fish variability to be accounted for by linear relationship with body length alone. The log transformed data, which assumes a power law relationship was also significant with a slightly higher predictive value ($R^2 = 0.54$) (Fig. 20). The parameters as determined from these data correspond to the following model, $y = 0.93x^{1.32}$.

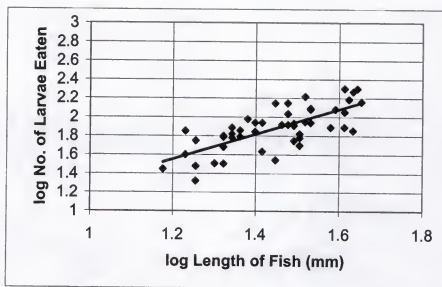


Figure 20. Log transformation of data assuming a power law relationship between fish maximum total body length and number of mosquito larvae eaten. ($y = 1.32x - 0.033$, $R^2 = 0.54$)

Discussion

Although the predictive value of the model is low, the relationship was highly significant. It is therefore reasonable to accept the power law relationship between the maximum total body length of an eastern mosquitofish and the number of fourth instar larvae consumed over a 24-hour period (n_p).

$$n_p = \frac{M}{m_{III}} = 0.93L(p)^{1.32}$$

This is not to imply that this formula represents some universal relationship between *Gambusia holbrooki* and *Aedes aegypti*. Rather, this should be thought of as a calibration of values of slope (e) and the constant (δ) for this particular experimental set-up. In a different sized arena, different temperature regime, different hunger level for the fish, or any one of a multitude of different variables used, one would expect e and δ to have different values. As long as the experimental procedure is kept as constant as

possible, then any changes to n_p , that occur when we add structure to the environment, can be attributed as being caused by the added structure.

Predator Size in a Complex Environment

Introduction

Previously, we had discussed the probability of any particular prey item h , being preyed upon ($P(Z_h)$) as a function of the probability of detecting the prey ($P(X_h)$) multiplied by the probability of the prey being accessible ($P(Y_h)$).

$$P(Z_h) = P(X_h) * P(Y_h)$$

The expected number of prey individuals consumed ($E(n)$) by a predator (p) of a particular body length ($L(p)$) should be the basic ingestion rate of the predator (n_p) multiplied by this probability.

$$E(n) = n_p P(Z_h) = \lambda L(p)^c P(X_h) P(Y_h)$$

where

$$P(X_h) \approx k \int_{-\infty}^{\infty} P(s) \left(\frac{n_i L(h_s)}{L(a_s) + n_i L(h_s)} \right) ds$$

and

$$P(Y_h) \propto 1 - r = 1 - \left(\frac{L(a_h) - L(a_p)}{L(a_h)} \right) = \frac{L(a_p)}{L(a_h)}$$

These formulae had been deduced as extensions of the assumption of a fractal paradigm. It should be possible to compare these predictions with actual values if we create a situation in which we allow the size of the predator to vary between arenas of differing complexity. The following experiments intended to test the assumptions and

the underlying paradigm by comparing the relative numbers of prey items taken under just such varying conditions.

Materials and Methods

Most of this experiment was set up in the same manner as the first experiment of this chapter. Fish, *Gambusia holbrooki*, and mosquitoes, *Aedes aegypti*, were collected and cultured as stated in the previous experiment, and glass battery jars, filled with 3 liters of well water were the experimental arenas. As in the previous experiment, 200 fourth instar mosquito larvae were hand dipped and placed into each jar and allowed to settle down for approximately one hour. A total of 108 individual fish were pre-selected so that 36 fell into each of three non-overlapping size classes. These were "small" (15 to 20 mm maximum total body length), "medium" (25 to 30 mm maximum total body length), and "large" (35 to 40 mm maximum total body length). As before, experimental fish were not fed for at least 48 hours prior to experimentation and room temperature was 78° F (25.6° C).

The only change to the arenas was that each jar contained either 50 g of a plastic plant or no plant at all. The three types of plastic plant were commercial products produced for the ornamental aquarium trade and were close visual mimics of the following plant species; *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Vallisneria americana*. This amount of "plant" material was chosen because it visually filled the available space and kept the mosquito larvae in close proximity to the plants but still allowed the fish to navigate the arena.

One fish was placed into each jar and the entire area was then surrounded by a drape of black plastic, although the fish were visible to each other. Twelve jars were

needed to cover every combination of fish size and cover type, and the experiment was repeated 9 times. Fish were removed after 24 hours and the surviving number of mosquitoes counted. It was assumed that any missing larvae were eaten. Partially eaten larvae were counted as eaten, but whole dead larvae were not counted, as it was not certain that they died from fish actions. In either case, both of these were a small fraction of the total number eaten.

Results

This is also a simple extension of the first experiment in this chapter, but this time involving two experimental variables, fish size and plant form. The response variable is number of mosquito larvae eaten. The results of this experiment are presented in Table 4 and Figure 21.

Table 4. Effect of plastic plant material on number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki*.

		Number of Larvae Consumed by Fish Size Class								
		small			medium			large		
		mean	n	s ¹	mean	n	s	mean	n	s
Plant form	none	52.0	9	21.1	101.4	9	26.0	120.8	9	58.7
	Vallisneria	49.6	9	16.6	94.6	9	28.6	98.1	9	60.6
	Hydrilla	63.7	9	27.7	79.3	9	32.4	60.6	9	29.9
	Myriophyllum	40.8	9	19.9	90.7	9	51.1	63.7	9	33.3
	total	51.5	36	22.4	91.5	36	35.3	85.8	36	52.2

¹s is standard deviation.

Table 5. Summary output 2-way ANOVA on effect of *Gambusia holbrooki* size and plant cover type on number of *Aedes aegypti* larvae eaten. Cover type; V = plastic *Vallisneria*, H = plastic *Hydrilla*, M = plastic *Myriophyllum*, No plant = no added cover.

SUMMARY	No plant	V	H	M	Total
<i>small fish</i>					
Count	9	9	9	9	36
Sum	468	446	573	367	1854
Average	52.0	49.6	63.7	40.8	51.5
Variance	446.3	275.3	768.8	394.9	499.6
<i>medium fish</i>					
Count	9	9	9	9	36
Sum	913	851	714	816	3294
Average	101.4	94.6	79.3	90.7	91.5
Variance	678.0	816.0	1049.5	2614.0	1244.9
<i>large fish</i>					
Count	9	9	9	9	36
Sum	1087	883	545	573	3088
Average	120.8	98.1	60.6	63.7	85.8
Variance	3449.9	3674.9	893.0	1108.8	2729.5
<i>Total</i>					
Count	27	27	27	27	
Sum	2468	2180	1832	1756	
Average	91.4	80.7	67.9	65.0	
Variance	2278.5	1973.7	904.4	1698.7	
ANOVA					
<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>
Fish size	33692.5	2	16846.3	12.5	0.000015
Cover type	12046.7	3	4015.6	2.98	0.035
Interaction	15188.7	6	2531.4	1.88	0.092
Within	129354.9	96	1347.5		
Total					

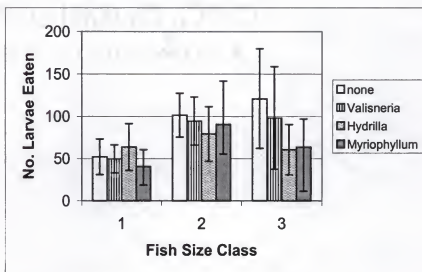


Figure 21. Mean number of mosquito larvae eaten out of 200 presented to eastern mosquitofish of three size classes (1=small, 2=medium, 3=large) in jars containing different types of plastic plant material. "None" indicates no plants present. Error bars represent $\pm$ one standard deviation.

A first glance at Figure 21 suggests that there might not be any real differences among treatments. Their standard deviations are high. But a 2-way ANOVA found the relationships to be highly significant (Table 5). As before, fish size had a highly significant effect on the number of prey eaten ($p < 0.000015$). The effect of plant form was also significant ($p < 0.035$). The question as to a possible interaction between predator size and plant form is more provocative. The statistical results did not reach the level of significance needed to proclaim a significant interaction ($p < 0.093$). Looking at the plot of the results (Fig. 21), we see that except for the Hydrilla-form with small fish, the presence of plant forms always hinders the fish. Additionally, except for Vallisneria-form, large fish were always more hindered than medium fish. This results in a bell-shape to the number of prey taken by fish size class plots.

Discussion

As interesting or suggestive as these results may be, they by themselves neither support nor negate the underlying model. While it is encouraging to note that both predator size and plant form affect the number of prey taken, the test of the model lies in comparing the expected numbers with those actually achieved. The first term in our formula for expected number killed is the base predation rate per day. This value had been previously determined as a power law function of predator length that fits the following formulae.

$$n_p = \lambda L(p)^6 = 0.93L(p)^{1.32}$$

If we take the midrange of the lengths for each of the predator size classes as the value for $L(p)$, we can predict n_p and compare it to the actual number of larvae eaten (Fig. 22). The trend line with the best fit to the data assumed a polynomial relationship between the actual kill and that predicted from n_p . Even that assumption only allowed for an R^2 value of 0.553.

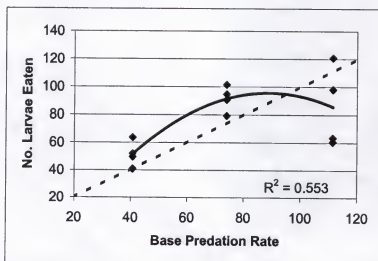


Figure 22. Mean number of *Aedes aegypti* larvae killed by *Gambusia holbrooki* in arenas with varying types of plant form expressed as a function of the predicted predation rates based on fish maximum total body length. Dashed line represents 1:1 relationship.

The term for detectability is more complicated. We do not know what the probability of a given scale occurring ($P(s)$) is. If we assume that the fish in this experiment rapidly learn to search for the monotypic prey presented to them, then we can estimate $P(s)$ as equal to one when s is equal to the mean size of the prey. The result is that detectability can be simplified to the following formula.

$$P(X_h | s = L(h_s)) \approx k \left(\frac{n_i s}{L(a_s) + n_i s} \right)$$

$L(h_s)$ was determined by randomly selecting 25 mosquito larvae from the same batch used in the experiments and measuring them. From this it was determined that the mean body dimensions of the experimental mosquitoes were 6.17 mm maximum length, excluding siphon, by 0.99 mm maximum width by 0.76 mm maximum depth for an average volume of 5.05 mm³. The cube root of this value (1.72 mm) was taken as the estimate of $L(h_s)$ when $L(h_s) = s$.

The length of the perimeter of the plant forms was not measured so we can not simply plug in the value of s to determine $L(a_h)$, but remember that each bundle of test plants weighed 50 gm and all were neutrally buoyant. This means that each bundle of plant forms had a volume of 50 cm³ or 50,000 mm³. Since the bundles "filled" the available space when submerged in 3 L (or 3.0×10^6 mm³) of water, a box-counting plot at this scale would have a count of 1 and an estimated perimeter of the cube root of this volume (or about 144 mm). Once, we have the estimated length at one scale in the box-counting plot, we can determine what the length would be at another scale providing we know the mean complexity (i.e., mean apparent dimension) between the two points.

The apparent dimension of real *Vallisneria americana*, *Hydrilla verticillata*, and *Myriophyllum spicatum* (Fig. 14 a,b,e) had been determined (see Chapter 3) and since

these plastic forms strongly resemble the real plants, their dimensions will be considered similar. The box-counting plots of these three plant species are reproduced here together for easy comparison (Fig. 23).

The measurements at the largest scales of this graph are beginning to approach the minimum line of existence (length = scale). If the plants scanned were in a bigger bunch, the shape of the plot at small scales would not change but would be moved up the y-axis. Therefore, assuming the plant does not develop a structure at larger scales, the slope can be extrapolated to account for larger patches of plant material. Mean D_A for the experimental plant forms can be estimated by taking the slope on these graphs from the scale of $L(h_e)$ to the minimum length value measured. These mean slopes ($1 - D_A$) can be used to estimate what the apparent length would be for our plant forms in accordance with the following formula.

$$\text{slope} = \frac{\text{rise}}{\text{run}} = 1 - D_A = \frac{\log L(a_2) - \log L(a_1)}{\log s_2 - \log s_1}$$

or

$$\log L(a_1) = \log L(a_2) - (1 - D_A)(\log s_2 - \log s_1)$$

This technique is only useful as an estimate for comparing the relative sizes of different objects at the same scale. A different technique for estimating the relative sizes of the same object at different scales will be discussed later. If we use this current technique to determine the apparent length of the different plant forms at the scale of a mosquito larva, we get huge numbers with a resulting negligible probability of random detection of larvae on these plants (Table 6).

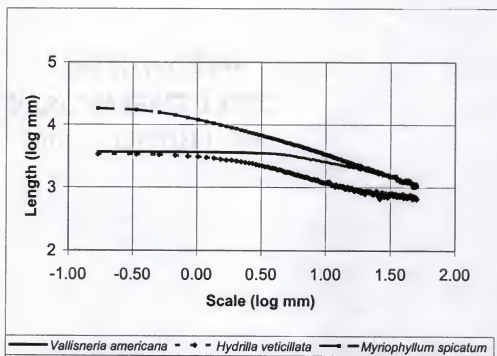


Figure 23. Box-counting plots of pressed and dried material from three species of aquatic plant as measured from two dimensional scans.

Table 6. Probability of random detection of prey items (h) as determined from comparison of relative lengths (see text for details).

	PLANT FORM			
	None	<i>Vallisneria</i>	<i>Hydrilla</i>	<i>Myriophyllum</i>
n_i	200	200	200	200
$I-D_a$	0.00	-0.36	-0.42	-0.67
s_h	1.72	1.72	1.72	1.72
$s_{3-liter}$	144.22	144.22	144.22	144.22
$L(a_{3-liter})$	0.00	144.22	144.22	144.22
$L(a_h)$	0.00	4.64×10^{52}	1.40×10^{63}	8.41×10^{98}
$P(X_i)$	1.00	7.40×10^{-51}	2.46×10^{-61}	4.08×10^{-97}

This is an instantaneous probability of detection and so it must be integrated across time to determine the overall probability of detection. The exact formula for the probability of detection over time is not known. Probability functions often take the following form.

$$P(X_i|t) = 1 - e^{-\lambda t}$$

where t is time and λ is the probability per unit time.

If this is the correct form for the probability function and if the formula for detectability is correct, then the log detectability added to the log predation rate should be proportional to the mean actual number of larvae eaten over any given time period.

$$\text{kill} \propto \log P(X_h) + \log(n_p)$$

If we plot these values (Fig. 24), we see that there is a slight tendency for increased detectability to increase the mean number of larvae eaten, but the regression predicts little of the variation ($R^2 = 0.145$).

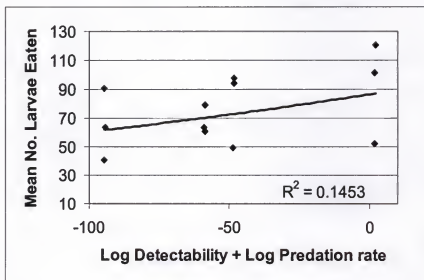


Figure 24. Mean number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* displayed as the log of (mean detectability $\times$ fish predation rate).

The third term in our formula for the expected number of prey items killed is the probability that the prey item is accessible ($P(Y_h)$) once it is detected.

$$P(Y_h) \propto 1 - r = 1 - \left(\frac{L(a_h) - L(a_p)}{L(a_h)} \right) = \frac{L(a_p)}{L(a_h)}$$

We already determined the length of the plant forms at the scale of the prey ($L(a_h)$) and we can use this to determine the length of the plant forms at the scale of the predator ($L(a_p)$). Looking at the box-counting plots prepared for pressed plant material in Chapter 3 (Fig. 23), it is apparent that as the scale decreases, each of the plant species approaches linearity at particular rates. If we increase the mass of plant material measured, we increase the total length but not the scale at which the plant attains linearity. To do that we would need to increase the size of the leaflets, not just increase the amount of plant material. This means that the apparent length of the plant at one scale divided by the apparent length at another scale would be a constant value. In other words, $\log L(a_h) - \log L(a_p)$ is a constant value. So, if we find out what this constant is on the plant material already measured, we can extend it to determine the values of $L(a_p)$ in our experiment. However, the question is open as to what the scale of a given predator should be.

The fish in this experiment were separated on the basis of maximum total body length but this does not represent the scale at which they interact with the prey. A more realistic limitation on the accessibility would be the gill-to-gill width of the fish. A series of 18 fish were taken and measured for total maximum body length as well as gill-to-gill width. These values were plotted against each other and a regression line fitted to the data (Fig. 25). The best R^2 value was obtained when it was assumed that the width of a given fish ($w(p)$) had a power law relationship to the total body length ($L(p)$), as in the following formula.

$$w(p) = 0.0281(L(p))^{1.47}$$

The gill-to-gill widths were determined from this relationship for each of the size classes of fish used in this experiment. These widths were compared to the data used to construct the box-counting plots and the mean length at that scale was determined for each of those plants over those ranges of width (Table 7).

The apparent length of the scanned images at the scale of the prey items ($L(i_p)$) was previously determined from the raw data used to create Figure 23. If we now subtract the apparent length of the scanned images at the scale of the predators from this value, we obtain our constants (Table 8). These constants, subtracted from the log length of their respective plant forms at the scale of the prey, will leave us with the estimated log length of the plant forms at the scale of the variously sized predators, which in turn allows us to calculate the index of accessibility.

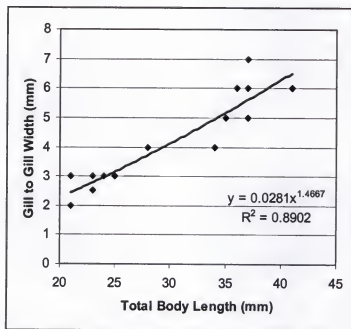


Figure 25. Power law relationship between the width and total body length of the eastern mosquitofish.

Table 7. Gill-to-gill width (mm) of fish and mean apparent length of plants (mm) at each size class of fish (maximum total body length) used in feeding experiments.

Size Class	Size Class Limits		Calculated Width		Mean Apparent Length of Plants $L(i_p)$		
	min	max	min	max	V.a.	H.v.	M.s.
small	15	20	1.5	2.3	3616.0	2686.0	9042.2
medium	25	30	3.2	4.1	3480.5	2096.3	6301.9
large	35	40	5.2	6.3	3137.0	1626.5	4821.2

Table 8. Determination of Index of Accessibility for *Gambusia holbrooki* feeding on fourth instar *Aedes aegypti* larvae in jars containing plastic plant forms. None = no added plants, V = plastic *Vallisneria*, H = plastic *Hydrilla*, and M = plastic *Myriophyllum*.

Plant Form	Fish Size ¹ Class	Mean L(image)		log constant	Mean L(experiment)		Accessibility index
		prey	predator		prey	predator	
none	small	0	0	0	0	0	1.00
	medium	0	0	0	0	0	1.00
	large	0	0	0	0	0	1.00
V	small	3613.6	3616.0	0.000	4.64×10^{52}	4.64×10^{52}	1.00
	medium	3613.6	3480.5	0.016	4.64×10^{52}	4.47×10^{52}	0.96
	large	3613.6	3137.0	0.061	4.64×10^{52}	4.02×10^{52}	0.87
H	small	2720.7	2686.0	0.006	1.40×10^{63}	1.38×10^{63}	0.99
	medium	2720.7	2096.3	0.113	1.40×10^{63}	1.08×10^{63}	0.77
	large	2720.7	1626.5	0.223	1.40×10^{63}	8.35×10^{62}	0.60
M	small	9374.1	9042.2	0.016	8.41×10^{98}	8.12×10^{98}	0.96
	medium	9374.1	6301.9	0.172	8.41×10^{98}	5.66×10^{98}	0.67
	large	9374.1	4821.2	0.289	8.41×10^{98}	4.33×10^{98}	0.51

¹ Fish size class based on maximum total body length.

If the number of larvae killed was influenced by their accessibility, then multiplying the index of accessibility by the base predation rate should provide us with an estimate of the expected number of mosquitoes killed. When we plot this expectation versus the actual number killed (Fig. 26), we find a strong relationship. The relationship,

which could be assumed to be linear with an R^2 value of 0.716, actually has the best R^2 value (0.731) if we assume a logarithmic relationship. The logarithmic shape indicates that predation is saturating, that there is a maximum achievable predation rate. This is consistent with an accessibility-controlled model. Increasing fish size leads to higher base predation rates but declining accessibility. This negative feedback would limit the rise in number of larvae eaten with increasing fish size.

On the face of it, this experiment indicates that predator size ($p < 0.000015$) and plant cover type ($p < 0.035$) had a significant effect on the number of mosquito larvae killed. Neither of these findings is particularly astounding. We had already estimated the relationship between fish size and number of mosquito larvae killed and it was presumed that plant material would have an impact on predation. But the point of this experiment was not to show that a relationship existed but rather to illuminate the nature of that relationship.

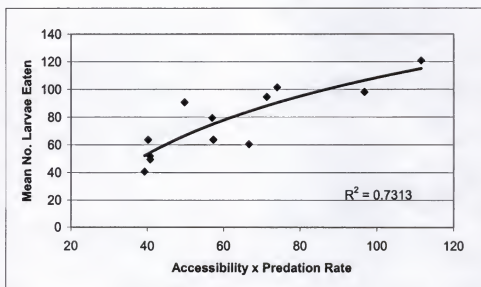


Figure 26. Relationship between mean number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* during experiments shown as a function of the expected number eaten as determined from accessibility of larvae to fish and base predation rates of fish.

It was heartening to see that plant form had a significant impact on predation but initially puzzling as to why the interaction between plant form and fish size was not statistically significant. But even allowing for *a posteriori* statistical manipulation, the best one can say is that an interaction is not strongly indicated. What this uncertainty seems to indicate is that even though plant form significantly impacts on fish predation, there is not a simple interaction between the various fish size classes and the level of impact by a given plant form.

The nature of the relationship between plants, predator, and prey begins to clarify when the parts of the relationship derived using a fractal paradigm are examined. The base predation rate, n_p , is just a transformation of fish body length and so it is not surprising that n_p fails to account for a great deal of the variation present when plant form is added to the experiment ($R^2 = 0.553$). But it does represent the expected number of prey taken when there is no plant present, so any impact needs to be measured against this expected value. Most revealing is that since a polynomial model best accounted for the variation between base predation rate and actual kill, the indication is that the true relationship is probably proportional to n_p multiplied by some other function.

This experiment indicated that detectability ($P(X_h)$) is probably not that other function. While it was possible to describe a linear relationship between the mean number of mosquitoes actually killed and the product of detectability and base predation rate (Fig. 24), this relationship described little of the variation ($R^2 = 0.145$). Accessibility ($P(Y_h)$) is a much likelier function for the other half of the polynomial. An assumed logarithmic relationship between the mean number of mosquitoes actually killed and the

product of accessibility and base predation rate (Fig. 26) described more of the variation ($R^2 = 0.731$).

This seems to indicate that detectability is not a concern and that accessibility on a complex surface is of paramount importance. In hindsight, it is perhaps not surprising that fish will have no problem detecting 200 mosquito larvae in three liters of water if given 24 hours to search. But detectability as deduced under a fractal paradigm is independent of predator size and is strictly a function of the relative lengths of prey to plant material. As prey size was kept constant while predator size was allowed to vary, this experiment may have inadvertently emphasized accessibility over detectability. To resolve this possibility, the experiments were repeated except that this time prey size was allowed to vary and predator size was kept constant.

Prey Size in a Complex Environment

Introduction

As in the previous experiment, this experiment is meant to examine the idea that the probability of any particular item h , being preyed upon ($P(Z_h)$) is a function of the probability of detecting the prey ($P(X_h)$) multiplied by the probability of the prey being accessible ($P(Y_h)$).

$$P(Z_h) = P(X_h) * P(Y_h)$$

and that the expected number of prey individuals consumed ($E(n)$) by a predator (p) and equals the base predation rate of the predator (n_p) multiplied by this probability.

$$E(n) = n_p P(X_h) P(Y_h)$$

The previous experiment had suggested that detectability ($P(X_h)$) was relatively unimportant and that the expected number of prey items killed can be accurately predicted as a function of the product of the base predation rate (n_p) and accessibility ($P(Y_h)$) alone. This experiment seeks to retest those ideas except that this time the fish will be presented with a greater range of detectability values.

Materials and Methods

Eastern mosquitofish (*Gambusia holbrooki*) and yellow fever mosquito larvae (*Aedes aegypti*) were collected and cultured as stated in the previous two experiments. Glass battery jars, filled with 3 liters of well water, were the experimental arenas. As before, experimental fish were not fed for at least 48 hours prior to experimentation and room temperature was 78° F (25.6° C).

Two batches of mosquito larvae were cultured so that one batch consisted of third and fourth instars larvae while the second batch consisted of first and second instar larvae. It proved to be impossible to count out fixed numbers of larvae for each jar. Preliminary experiments showed that the fish were capable of consuming well over 1000 of the younger larvae within a 24-hour period. The time required to count out this many larvae would have resulted in a significant portion of the larvae molting into the third instar. To resolve this, it was arranged that each arena would be stocked with a constant volume of mosquito larvae. Larvae were scooped up out of the rearing containers using a fine mesh net. The ball of larvae was allowed to drain for a few seconds and a measuring spoon was used to select a level 1/16 tsp (approx 0.31 ml) of larvae for each arena. Two additional spoonfuls of larvae from each age group were directly preserved in alcohol and were manually counted at a later date to calibrate the number of larvae presented in each

arena. Mosquitoes were allowed to settle down for approximately one hour before fish were added. Individual fish were pre-selected to fall into the "medium" (25 to 30 mm maximum total body length) size class of the previous experiment. This size class of fish was chosen because the previous experiment indicated that they were more affected by the plant material than the small size class but were not dominated by questions of accessibility like the large size class. Only female fish were utilized in this experiment.

The arenas were set up with plastic plant forms just as in the previous experiment. An experimental run of 24 jars was repeated on three different dates. This resulted in three repetitions for each larvae size/plant form combination on each date, with a total of 9 repetitions over the course of the entire experiment. One fish was placed into each jar and the entire area was then surrounded by a drape of black plastic. Fish were removed after 24 hours and the surviving number of mosquitoes counted. The number of mosquitoes eaten was estimated as the mean number of mosquitoes in the preserved samples minus the number of surviving larvae. This also allowed us to estimate the mean volume of the individual mosquito larvae. The older and larger batch of larvae had an estimated mean volume that ranged from 0.49 to 0.63 mm³ over the three dates, while the younger batch of larvae ranged from 0.11 to 0.22 mm³ mean volume.

Results

This experiment is similar to the last experiment except that this time the two experimental variables are prey size and plant form, and fish size is kept constant. The response variable is percent predation of mosquito larvae. The results of this experiment are presented in Table 9 and Figure 27. Table 9 seems to indicate that there is not much difference between the mean percent predation rates for the experimental treatments and 2-way ANOVA seems to uphold this (Table 10). While there is a statistically significant

effect of varying plant form on predation, there is no significant difference in the percent predation between the larval size classes.

Table 9. Percent predation on *Aedes aegypti* larvae by medium sized *Gambusia holbrooki* (n = 9 for each plant form/larval size combination).

Plant Form	Small Larvae		Big Larvae	
	mean	sd	mean	sd
none	68.6	19.5	75.8	20.5
<i>Vallisneria</i>	57.6	15.8	44.6	38.5
<i>Hydrilla</i>	56.3	14.3	54.1	19.1
<i>Myriophyllum</i>	51.1	23.5	53.4	17.1

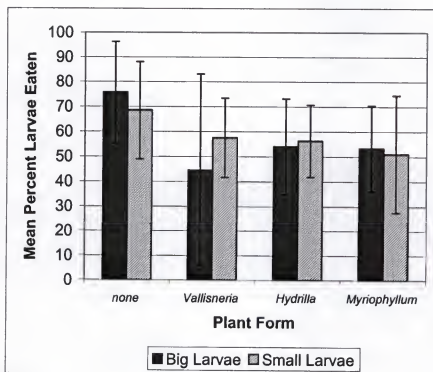


Figure 27. Percentage of big (0.49-0.63 mm³) and small (0.11-0.22 mm³) *Aedes aegypti* larvae preyed upon by medium sized (25-30 mm maximum total body length) *Gambusia holbrooki*. Error bar represents ± 1 standard deviation.

Table 10. Summary output 2-way ANOVA on effect of *Aedes aegypti* larval size and plant cover type on number of larvae eaten by *Gambusia holbrooki*. Cover type; None = no added cover, V = plastic *Vallisneria*, H = plastic *Hydrilla*, M = plastic *Myriophyllum*.

SUMMARY	Plant Cover Type				Total
	None	V	H	M	
<i>small larvae</i>					
Count	9	9	9	9	36
Sum	6.17	5.18	5.07	4.60	21.02
Average	0.69	0.58	0.56	0.51	0.58
Variance	0.038	0.025	0.021	0.055	0.036
<i>big larvae</i>					
Count	9	9	9	9	36
Sum	6.82	4.01	4.87	4.80	20.51
Average	0.76	0.45	0.54	0.53	0.57
Variance	0.042	0.149	0.036	0.029	0.072
<i>Total</i>					
Count	18	18	18	18	
Sum	12.99	9.19	9.94	9.40	
Average	0.72	0.51	0.55	0.52	
Variance	0.039	0.086	0.027	0.040	

ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Larvae size	0.0036	1	0.0036	0.073	0.79	3.99
Cover type	0.52	3	0.17	3.52	0.020	2.75
Interaction	0.10	3	0.034	0.68	0.57	2.75
Within	3.16	64	0.049			
Total	3.78	71				

This experimental setup confounds size of prey item with density of prey item, but Figure 27 does not consider density. We had previously deduced that the probability of detecting a prey item was at least partially a function of the number of prey items presented. This comparison also loses precision by lumping all mosquito larvae into either big or little categories. Variables in larval rearing procedure included initial

stocking density, amount of food provided, and time before experimentation. Slight changes in these variables resulted in three sizes of big larvae (0.49, 0.59, and 0.63 mm³) and three size classes of small larvae (0.11, 0.14, and 0.22 mm³), so that each cover type class was paired with three repetitions of six distinct larval size classes. If we plot the number of each actual size class eaten, instead of the percentage, we get a fair representation of an exponential function (Fig. 28).

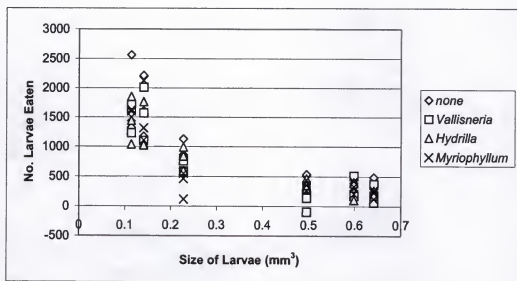


Figure 28. Estimated number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* under cover of different plant forms.

If the actual number of prey killed has an exponential relationship to the average size of the individual prey item, then this relationship can be expressed according to standard notation for an exponential function.

$$n = \beta_0 e^{-\beta_1 s}$$

This would mean that the natural logarithm of the number of prey killed ($\ln n$) would have a linear relationship to the size of the individual prey item (s). Such a model

has a fairly high R^2 value for each of the cover types examined: none $R^2 = 0.822$, *Vallisneria* $R^2 = 0.717$, *Hydrilla* $R^2 = 0.840$, and *Myriophyllum* $R^2 = 0.592$. The R^2 values suggest that an exponential relationship is close to the truth, but the lower values for some of the cover types suggest something else is affecting the results. If we examine the log linear plot of just the regression lines (Fig. 29), we see that cover type seems to have an effect.

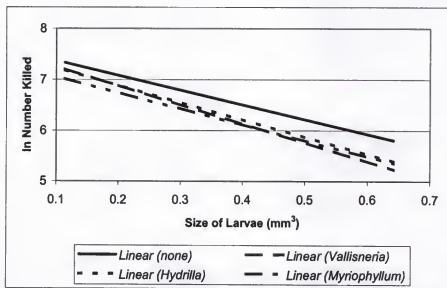


Figure 29. Regression lines for plot of $\ln$ number of larvae eaten as a function of mean individual larval size.

Discussion

This experiment was initiated to reevaluate the previous experiment over a greater range of detectability values. The nature of the arena makes this impossible to do without also affecting the base predation rate and the accessibility. Each of these three factors must be considered in order to evaluate how closely the actual number of larvae eaten matches up with that predicted from the following model.

$$E(n) = n_p P(X_h) P(Y_h)$$

The base predation rate (n_p) had been determined in a previous experiment to have a power law relationship with fish maximum total body length ($L(p)$) that was calibrated as follows.

$$n_p = \lambda L(p)^e = 0.93L(p)^{1.32}$$

For the medium sized fish used in this experiment, body length averaged 27.5 mm and n_p equaled 74.00 larvae over a 24-hour period. But this was for fourth-instar larvae with a mean volume of 5.05 mm³. The larvae used in this experiment were smaller than that and so should support higher n_p values. If we assume that each fish consumes a constant volume of food per day (M) and that size of larvae does not affect any aspect of their digestibility, then the daily predation rate on a particular prey (n_{pi}) can be determined for prey of any mean size class (m) (Peters 1983).

$$n_p = \lambda L(p)^e = 74.00 = \frac{M}{5.05}$$

$$M = 74.00 \times 5.05 = 373.95$$

$$n_{pi} = \frac{373.95}{m}$$

A plot of the estimated number of larvae killed in the experiment as a function of the predicted kill from base predation rates, results in a fairly strong relationship with an R^2 value of 0.780 (Fig. 30).

Clearly, much of the variation between the larval size classes in number killed by a predator can be explained as a simple result of more small larvae being needed to make up the daily ration. The implication is that changing the size of the prey had little to no effect on detectability and accessibility. Adding the factors of detectability or accessibility and seeing whether this improves the descriptive power of the model can

test this. Recall that by granting certain assumptions, detectability and accessibility were described by the following formulae:

$$P(X_h) = k \left(\frac{n_i L(h)}{L(a_h) + n_i L(h)} \right)$$

and

$$P(Y_h) = \frac{L(a_p)}{L(a_h)}$$

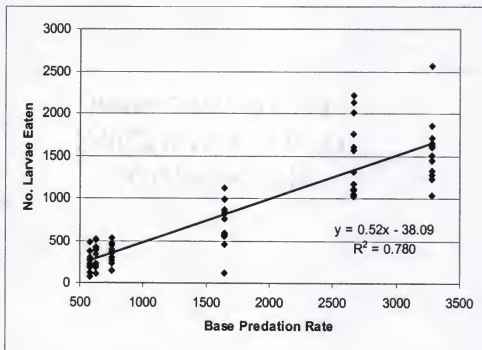


Figure 30. Estimated number of larvae eaten in each jar presented as a function of the base predation rate as determined from larval size.

To determine detectability and accessibility for any given plant form, we need to determine the number of prey individuals present, the scale of six different size classes of prey ($L(h)$), the length of plant-form material as measured at those six scales ($L(a_h)$), and the length of plant-form material as measured at the scale of the predator ($L(a_p)$). The

calibration of the standard number of larvae presented to the fish provides us with the values for n_i , and $L(h)$ is just the cube root of the mean volume for an individual prey item. As in the previous experiment, we can use the box-counting plot of the pressed plant images to determine $L(a_h)$ for the plastic plant forms.

As there are six size classes of prey, there will be six values of $L(h)$. If we call the smallest scale $L(h1)$, we can find the mean slope on the box-counting plot from $L(h1)$ to the minimum value. We previously determined that a single box with a scale of about 144 mm could cover the experimental jars resulting in an apparent length of 144 mm. If we extrapolate to the smaller scale $L(h1)$, using the mean slope we had determined from the box-counting plot, we obtain an estimate of $L(a_{h1})$. We can now determine any $L(a_{hi})$ by realizing that for any patch of repeated form, $\log L(a_{hi}) - \log L(a_{h1})$ is a constant with regards to extent of patch as long as the individual forms are unchanged. We can determine these constants from the box-counting plots and use them to calculate $L(a_h)$ for scales $L(h2)$ through $L(h6)$.

The resulting values for detectability were extremely small mandating the need to plot mean kill as a function of the logarithm of detectability (Fig. 31). The plot appears to show no relationship. However, unlike the previous experiment, each plant form had predation numbers for six different detectability levels. This means that it is possible to create a plot of log detectability versus the number killed for each plant form tested. The regression line for each plant form had high R^2 values if a polynomial relationship was assumed (Figs. 32-34).

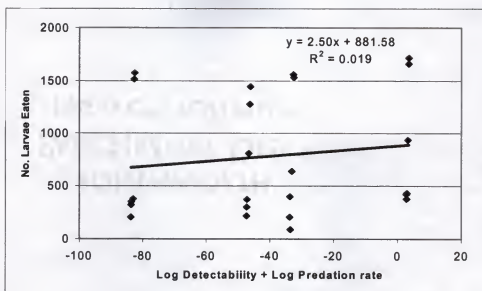


Figure 31. Mean number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* displayed as a product of mean detectability and fish predation rate.

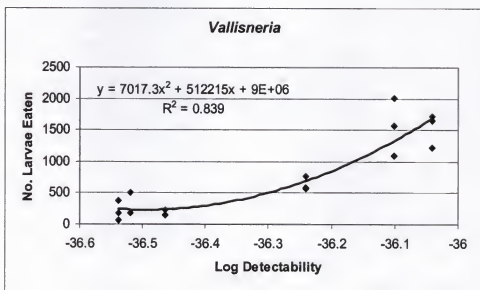


Figure 32. Number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* in and around *Vallisneria*-form plastic plant material expressed as a function of detectability. Regression line assumes a polynomial model.

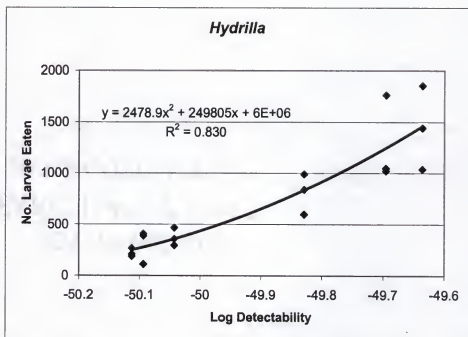


Figure 33. Number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* in and around *Hydrilla*-form plastic plant material expressed as a function of detectability. Regression line assumes a polynomial model.

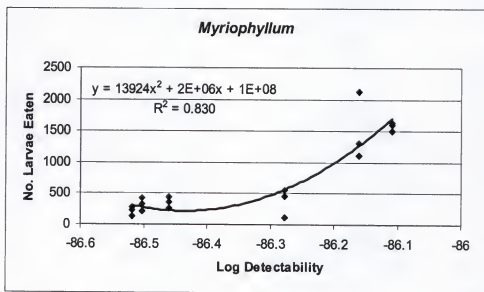


Figure 34 Number of *Aedes aegypti* larvae eaten by *Gambusia holbrooki* in and around *Myriophyllum*-form plastic plant material expressed as a function of detectability. Regression line assumes a polynomial model.

While the regression lines do explain much of the variation, the fact that a polynomial model had the best fit implies that the relationship is being arrived at indirectly. It is as if the elements that were used to construct the detectability index are important in determining the number of larvae killed but should be combined in some other manner or in conjunction with some other function.

Accessibility as a potential function controlling the expected kill had already been discussed in the previous experiment. While keeping the predator size constant helps to minimize the effect of accessibility, it cannot be completely excluded. This is because accessibility is not completely independent of detectability. The length of the arena at the scale of the prey item ($L(a_h)$) is included in both functions. The values for length of the arena at the scale of the predator ($L(a_p)$) are needed to determine accessibility of a given prey item. The log difference constant method can be used to determine this since the relative sizes of the same object are being determined at different scales. Once this is accomplished, the mean number of larvae eaten can be plotted as a function of the product of accessibility and base predation rate (Fig. 35).

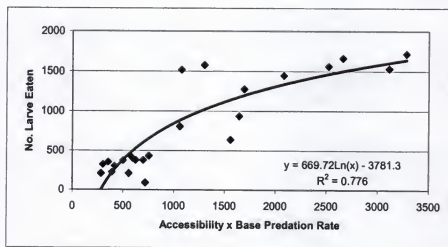


Figure 35. Interaction between accessibility of prey and base predation rate of fish on the mean kill achieved. Regression line assumes a logarithmic model.

As in the previous experiment where predator size was varied, varying prey size results in a logarithmic relationship between the mean kill and the accessibility-base predation rate product. The results are even more interesting if all data points are considered instead of mean number of larvae eaten, and the plant forms examined individually (Figs. 36-39). Of course in this situation, the plot for "none" cover type is just base predation rate versus actual number eaten since accessibility is 1.0 at all scales. In all these cases, except for the *Myriophyllum*-form, a straight-line model regression provided the highest R^2 values. Even in the *Myriophyllum*-form, a straight-line model regression had a high R^2 value. The data suggests that for any given plant form, number of prey items killed over a unit period of time will be a constant function of the base predation rate of the predator multiplied by the accessibility of the prey item.

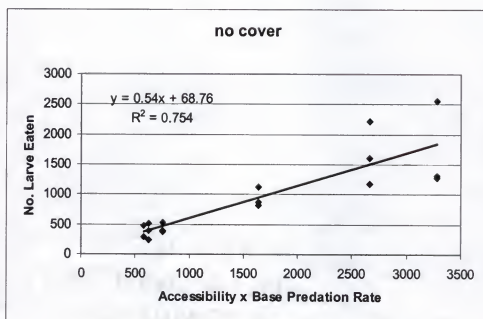


Figure 36. Interaction between accessibility of prey and base predation rate of fish on the number of larvae eaten without cover.

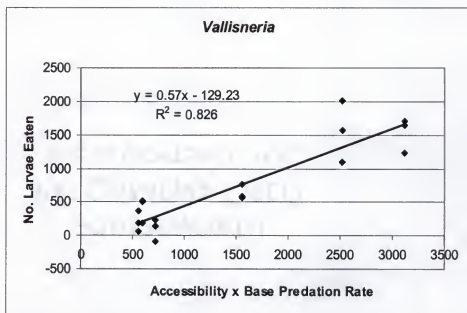


Figure 37. Interaction between accessibility of prey and base predation rate of fish on the number of larvae eaten in *Vallisneria*-form plant cover

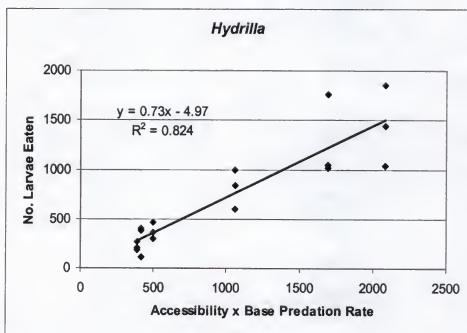


Figure 38. Interaction between accessibility of prey and base predation rate of fish on the number of larvae eaten in *Hydrilla*-form plant cover

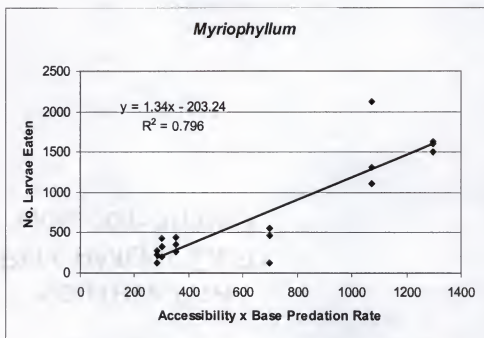


Figure 39 Interaction between accessibility of prey and base predation rate of fish on the number of larvae eaten in *Myriophyllum*-form plant cover.

At this point, the question should arise in the reader's mind that if accessibility is a universal way of considering and comparing the shapes of plants and how they affect predation, why should there be differences between the plant-forms in the manner that accessibility impacts predation? I believe that the answer lies in the way the box-counting plots were done. All counts were done on two-dimensional scans, which is why we used length of arena rather than surface area. Our estimates would have been fine if we could have assumed the fish had no added difficulty perceiving the prey along the third dimension, but clearly there is an added level of difficulty that should increase the magnitude of the kill vs. accessibility-predation rate slope. In fact, the magnitude of this slope should be proportional to the complexity of the plant-form. If these slopes are compared to the apparent dimension of the plant forms measured in Chapter 3, one sees that this is indeed the case (Table 11). In other words, the accessibility impact was

disproportionately greater for large fish on the more complex plants than on less complex plants, indicating that the failure to compare accessibility across plant forms is consistent with a failure to measure the third dimension.

Table 11. Comparison of slope of regression line from number of larvae eaten vs. (accessibility x base predation rate) chart to apparent dimension of plant forms (D_a).

	slope	D_a
None	0.54	0.00
<i>Vallisneria</i>	0.57	1.04
<i>Hydrilla</i>	0.73	1.30
<i>Myriophyllum</i>	1.39	1.52

Conclusions

A lot of the arguments within this chapter rely on there being a power law relationship between the size of the predator and the amount of prey items consumed. Fortunately, this relationship has been well documented and shown to be fully explainable using metabolic arguments alone (Peters 1983). One advantage of this for the current study is that one does not have to consider changes in predation rate as a behavioral change with fish size. Certainly behavior plays a role, but if it is a physiological response, then one can think of this as the base line. While the addition of plants forms may cause an initial behavioral change, the course of time will drive the fish to approach their physiological norms. Resulting deviations from these norms can be more readily attributed to physical rather than psychological impediments to the predators.

The disadvantage of metabolism as the driving function to the power law is that anything that can change the metabolism of the fish can affect the variation in our calibrations. An individual fish's physical health or reproductive status can vary even over the 24-hour period of any given experiment. The result is considerable variation in the individual predation rates and an overall fuzziness in determining the exact relationship, shown by the relatively low R^2 values of the calibration experiments ($R^2 = 0.54$).

Exact relationships aside for the moment, there is a clear effect of changing plant material on predation rates. Loosely stated, the presence of plant material has a negative impact on predation rates. This impact seems to scale with changes in size of predator or prey in a non-linear fashion. The effect of a given plant form seemed to vary not only with predator size but also type of plant form. These effects seemed to agree with what had been predicted by the concepts of detectability and accessibility.

Detectability and accessibility had been deduced as extensions of the Richardson effect. The Richardson effect, the cornerstone of fractal geometry, states that the apparent size of an object is strictly relative to the scale of measurement. Box-counting had shown that the plant forms studied here, while not fractal in the strictest definition of the term, can be considered as complex surfaces which show the Richardson effect over a wide range of scales.

Accessibility was taken as the ratio of the size of the plant apparent to the predator divided by the size of the plant apparent to the prey. Both the experiment with variable predator size and the experiment with variable prey size had strong correlations between the product of (accessibility X basal predation rate) and the actual number of

larvae killed. This is good indication that accessibility has a real impact on the survival of a prey item once detected.

Detectability was taken as the ratio of the unit size of the prey items divided by the size of all other objects in the arena, measured at the scale of the prey. It was assumed that the predators hunted at the scale of the prey item and that prey items were instantly recognized once detected. As defined here, prey detectability is independent of predator size, so it is of no real surprise that the experiment with variable predator size failed to find any relationship between detectability and number of prey killed. The experiment with variable prey size does provide some evidence for detectability being at least partly effective in determining the number of prey items killed but only in a form specific manner. Possibly one of the assumptions had been violated but a more likely explanation is that this experimental setup is not a powerful test of the impact of detectability. The arenas are small, the prey is motile, and the predators have an entire day to search. It is not unreasonable to assume the fish will have little trouble detecting the mosquitoes in this situation. Detectability may have its greatest impact over larger scales such as a fish's relative success between patches of plant material rather than success within a patch where it is overwhelmed by the functions for accessibility.

Given the strong evidence for the impact of accessibility and the weaker evidence for the impact of detectability on predation, the next question should be what does this mean to the animals involved. Accessibility is strongly influenced by the size of both predator and prey. From the prey's perspective, complex habitats increase the amount of inaccessible space and slight changes in prey size increase this advantage. From the predator's point of view, any adaptation for reaching into small openings would help to

negate this advantage. In simple areas, accessibility offers little or no protection, so that this is not a reason for prey or predators to be small. Detectability on the other hand, is independent of predator size but influenced by prey size and prey number. In simple habitats the accessibility is high so prey need to be small and dispersed to keep detectability down but predators can be large. In the simplest of arenas, both detectability and accessibility are almost certain so that other anti-predator devices would need to be employed.

The suggestion is that certain levels of complexity will have profound impact on the structure of the animal community. A complex area such as a coral reef or dense vegetation patch should be dominated by disproportionate numbers of clumped small prey species and predators with odd feeding adaptations such as extended snouts. Large predators with big mouths should dominate simpler areas while the prey will be sparse and dispersed. Prey species will be either small or have some adaptation to avoid being eaten. How close are these predictions to the situation found in nature? The next chapter reviews the literature on this very question.

CHAPTER 6

REVIEW: PREDATION AND COMMUNITY

The previous chapter quantified the impact of arena on predation. While the formulae were new, the underlying concept that a plant or any structure interferes with predator and prey relationships has been recognized for a very long time. The classic bottle experiments of Gause (1934) showed that *Paramecium* can only coexist with *Didinium* when refuges for the prey are provided or prey are constantly introduced or when the predator-prey contact is otherwise reduced. This latter condition can be achieved by making the medium more viscous or by increasing the total system volume. This suggests that added structure helps to minimize the contact between predators and prey. Structural complexity can decrease predation pressure by providing either absolute (preventing contact) or relative refuge (reducing contact). If prey exhibits any sort of active predator avoidance, structure may facilitate this. This reduction in prey vulnerability has been called "resource depression" when viewed at from the predator's point of view and "enemy free space" when viewed from the prey's point of view. Ware (1972a,b) found it to be a real phenomenon in that intensity of predation and total food consumption are inversely related to complexity of the substrate.

If structure reduces predation risk, then selection will act to enforce the association of prey with structure. Cooper and Crowder (1979) list several examples of poorly defined 'complexity' affecting some aspect of predation. The crux of their argument is that structural complexity tends to reduce capture efficiency resulting from increased search and pursuit times. This results in benthic prey biomass increasing with

increasing structural complexity. The reduced capture efficiency would allow prey items in the vegetation to be larger and/or more mobile than those obtained from predator gut analyses. Any prey item that is for any reason more "vulnerable" should be more closely associated with structure than less "vulnerable" prey. In more simple terms, the suggestion is that structure in the habitat entrains the prey population. If this is the case, then the "shape" of the environment should help to determine the "shape" of the animal community.

How Do You Measure Community Shape?

The previous chapter showed that predation interacts with habitat complexity in a scale dependent manner. The shape of the prey community should vary over scale in a manner that reflects that complexity. But is this necessarily so? To what extent can small independent acts of predation result in an overall community shape?

Chapter 3 explored the perception and measurement of complexity and developed box-counting as a technique for expressing complexity. While chapter 3 showed that an average individual response to a shape could be mathematically predicted, chapter 5 showed that predator and prey interacting across a shape were also governed by the underlying complexity of the shape. This chapter examines previous studies that can be considered as taking this progression one step forward. Here we will consider entire communities of predators and prey and attempt to show that their structure is determined at least in part by the underlying complexity of the arena. Our first hurdle is to determine what we mean by community.

The term community has been defined as a naturally occurring, mutually sustaining, interacting assemblage of plants and animals living in the same environment

and fixing, utilizing, and transferring energy in some manner (Smith 1980). Clearly no community can continue to exist without the inclusion of animals, plants, protists, monerans, fungi, etc., yet at the same time, no one could possibly census every single living species in a given area. Even if possible, the census would need to be conducted over a defined area. This can result in further problems of definition since no definable habitat is completely isolated from all the other habitats and is in fact itself dividable into further "micro" habitats. For example, consider a lake, although definable as a separate unit, it receives input and loses material to streams, the atmosphere, and the surrounding terrestrial habitat. While, it is easy to include the fish that live in the lake, the question arises if we should include the fish that travel through the lake on their way upstream. What about frogs and turtles, which live in and out of the lake? Is the Kingfisher part of the terrestrial community where it lives and breeds or is it part of the lake community where it obtains its food? Any research project needs to limit the taxonomic and geographic scope of the study. So the question remains, how does one measure the shape of a narrowly defined portion of the community?

Richness and Diversity

Just about the simplest way to examine a given community is to count the number of species in it. This value is termed the richness so that if one community has more species than another, it is said to be richer than the other community. The problem is that this statistic is extremely sensitive to sample size. A large sample is more likely to contain some of the less common species and show an apparently higher richness value. This means that even if two samples are drawn from the same community, the large one will probably have a higher richness.

To work around this problem, Benson and Magnuson (1992) measured fish richness in Wisconsin lakes using Rarefied Species Richness (RAR), which is determined as the expected number of species caught if the number of individuals caught had been 50. This was done to control for the effect of different sample sizes between lakes. A complication with this method is that density and diversity of the fauna begins to impact on RAR. Density is usually used to compare several species across two or more habitat types. If a given species has low density, it will drop out of the RAR count but if all species have low density, RAR will be high. In other words, if overall diversity is low, then one or two species are dominating the community and will represent most of the 50 specimens used to calculate RAR. If overall diversity is low, no species are dominating and the 50 specimens begin to represent more species.

Even if two communities have the same richness, it does not tell us much about them in terms of structural similarities. One community might have its constituent species occurring at roughly equal numbers, while the other may be heavily dominated by one or two species. Diversity indices were developed to examine questions of heterogeneity in species number and abundance within a community. The most widely used index is the Shannon-Weiner Index (Shannon and Weiner 1963), which is derived from the following formula.

$$H = -\sum_{i=1}^s (p_i)(\log p_i)$$

where s = number of species, i = species number, and p_i = the proportion of individuals in the sample belonging to the i th species. The Shannon-Weiner Index is an indicator of how well one could predict the species of an individual drawn from the sample. The

lowest value is 1 in which all members of the population belong to the same species. The index is highest when all members belong to a different species.

Without getting into the debate as to the value of diversity indices, it should be noted that collapsing all of the frequency information of every species into a single statistic represents a significant loss of information. An index does not tell us anything about the absolute number of individuals nor does it tell us anything about the mass of individuals in the community. This information can only come from looking at the frequency distribution of the community.

Size Versus Frequency

In an animal community shape study, there are typically three quantities under consideration. One can consider the number of individuals, the number of species, and the mean mass of the animals involved. While there are variations and nuances in the presentation of the data, there are essentially only three types of comparisons typically made. One type of study is to rank the number of species by the number of individuals they contain. A second type can consider the number of individuals present as a function of their mass, regardless of their species. The third type is to plot the number of species present over a given range of body mass.

A plot of the number of species per given abundance class is called a species:abundance or species: frequency distribution. These types of graphs were first developed by Preston (1948) and Williams (1953) and were later refined by May (1975, 1981), but interested readers should also consult Southwood (1978) and Sugihara (1980). Initially, the number of species within a given abundance class was thought to be represented by a geometric progression (Preston 1948) but was later shown to be best described by a lognormal model (Williams 1953). May (1981) developed the lognormal

model further. If the number of species is plotted as a function of the log of their relative abundance then the resulting graph is almost always lognormal. To quote May directly "there is a bell-shaped gaussian distribution in the logarithms of the species' abundances". The Central Limit Theorem holds that any distribution resulting from interplay of many, more or less, independent factors will always be lognormal in shape. Other shapes do occur and these can reveal biological facts rather than some statistical quirk. For instance the old-field succession study of Bazzaz (1975) in which the relative cover values of different plant species was plotted as a function of their rank abundance. Initially, the plot of species resembles a straight line, but as the years progress and more and more species enter the old-field study sites, the shape begins to change. A plot of a field that had been left for 40 years finally resembled the sigmoid S-shaped curve of a log normal distribution. Studies of communities undergoing pollution show the reverse of this process.

Not many studies consider the community as a collection of individuals. As biologists, we hesitate in considering a 1-g fish as being equivalent to a 1-g beetle, yet they may be equivalent within certain ecological parameters. Several studies have found patterns in communities considered as individuals or biomass over different body-size classes (Janzen and Schoener 1968; Janzen 1973; Morse *et al.* 1985; Griffiths 1986; Rodriquez and Mullin 1986; and Strayer 1986). The most common pattern observed is a rapid rise in numbers with increasing body size followed by a slow asymptotic approach to zero. It is difficult to interpret this kind of distribution because of the high peaks and long tail. To ease comparisons, it has become standard practice to consider log number of individuals (or log biomass) across log body-size classes. This type of comparison has

its origins in the work of Hutchinson and MacArthur (1959), which will be discussed in greater detail later in this section. In general, these abundance: body-size distributions were developed as a means to consider the relative success values of different species (Damuth 1981; Peters 1983; Peters and Raelson 1984; Peters and Wassenberg 1983; and Brown and Maurer 1986).

Occasionally, these results appear to be sensitive to scale in that patterns observed over large areas break down when restricted in range. Peters and Raelson (1984) found that log abundance as a function of log body mass shows a strong linear regression for all mammal species when considered on a worldwide scale. On a global regression, log body mass accounts for about 70% of the variability in log abundance. However, as the geographic region is restricted in scope, the relation becomes weaker, and it becomes impossible to predict the abundance of an individual species based on size.

Another way to consider the same data is to plot the total biomass of all species present within a range of body size classes. Maurer and Brown (1988) plotted the entire North American avifauna in this manner. Previous studies suggested that biomass would be distributed evenly across the body mass classes, but the North American birds do not show this type of distribution. Rather, biomass was found to increase with increasing body mass class even though the density of species was decreasing.

Edgar (1994) conducted one of the most detailed studies of this type. He examined the benthic community in marine habitats by measuring the biomass captured by sieves of varying size. He found that when log biomass of the benthic community is plotted against log sieve size, a trough in body mass often occurs at ~ 10 :m in diameter, with an additional trough in biomass at ~ 1000 :m. Causes are equivocal but note that

these ranges are roughly where microbes overlap with meiofauna and where meiofauna overlaps with macrofauna. No gaps were found in the size structure of macrofauna of the major macroalgal, seagrass, and bare sediment habitats present around Australia and Japan. All plots were nearly linear with a negative slope. The slope of this relationship increases (i.e., becomes less negative) as the proportion of larger animals increases. This led Edgar (1994) to propose the slope as a community size-structure parameter called size-dominance. It is written as G with the subscript telling the size range examined. In other words, G is recognized as being scale specific.

Edgar (1994) also compared data to previous studies by Warwick (1986) and Clarke (1990). These earlier authors used the parameter W , which is calculated using the following formula.

$$W = \frac{2(\rho_A - \rho_B)}{(S - 1)}$$

where ρ_A and ρ_B are the average species rank for abundance and biomass and S is the total number of species in the sample. Changes in G corresponded closely with changes in Clarke's (1990) index W (cross correlation coefficient $r = 0.76$, $n = 25$, $p < 0.001$). On closer examination, it is apparent that the two values will only differ significantly if one of the most common animals also happens to be one of the largest.

The ideas of size dominance across scale had led researchers to measure the size distribution of the whole faunal assemblage as if it occurred on a fractal surface. Significant correlations have been found between the slope of size-abundance curves and the dimension of the surface. This has been found to be the case for insects on plant surfaces (Morse *et al.* 1985), arthropods on lichens (Shorrocks *et al.* 1991), spiders on

trees (Gunnarsson 1992), and arthropods in soil (Kampichler 1993). The goal in these types of studies is, that by knowing one of either the size-abundance of the fauna or the dimension of the surface, to be able to predict the other. As yet, the predictive ability is limited and much work needs to be done.

The third type of comparison that is frequently made for community structure is to consider the number of species present in a given body size class, regardless of their individual abundances. A plot of how many species are in different body size categories is called a species:body-size distribution. This type of plot was first developed by Hemmingsen (in Peters 1983) but is best known from the work of Hutchinson and MacArthur (1959). May refined many of the concepts and techniques (May 1978, 1981, 1986), but interested readers should also consult Griffiths (1986). Hutchinson and MacArthur (1959) proposed a model in which the number of species in a given biotype rapidly increases with increasing body size until the modal value had been reached, after this there is a slow decline in number, "ideally asymptotic to unity" as the size increases. Maurer and Brown (1988) considered the entire avifauna of North America. The frequency distribution of species with respect to body size ($\log_2$ octaves) in the North American fauna agreed qualitatively with the form predicted by Hutchinson and MacArthur (1959). The distribution was unimodal and decreased asymptotically but was skewed towards larger body size categories.

May (1978) matched data to this model and formalized the appearance of the species:body-size distribution. If one plotted the number of species (S) per $\log_2$ size class of some linear measure (L) (not necessarily length), then the portion of the plot from the mode and larger will scale as approximately L^{-2} . $\log_2$ size classes are used simply for the

convenience of saying that one size class is twice as large as the previous. As long as only one particular type of animal was being examined (e.g., all mammals or all beetles), there was a good visual match between the predicted and the observed slope. However, no statistical test was done to confirm the similarities. May's (1978) explanation for the appearance of these plots is that animals perceive and divide their environment in a 2 dimensional manner and that to account for an animal's extension into three dimensional space (i.e., volume) one may wish to use the more general form of $S \sim L^{-y}$, where $2 \leq y \leq 3$.

Morse *et al.* (1988) plotted log number of species of arboreal beetles versus log body length class and found that the species:body length distributions are similar to those found by other authors (Hemmingsen 1934 (in Peters 1983); Schoener and Janzen 1968) in being approximately a log-normal distribution. Under a log-log plot, the upper tail of the distribution showed a near linear decline, which indicated a power law relationship between number of species and their body length. The slope of the upper tail of their distribution was $-2.64 (\pm 0.38)$, which is reasonably close to Hutchinson and MacArthur's (1959) predicted value of -2 . Other studies have shown that above a certain threshold, the number of species scales as body length⁻² (Terakawa and Ohsawa 1981; Erwin and Scott 1980; and Erwin 1983). Morse *et al.* (1985) contended that the explanation for the slope being less than 3 instead of 3 is that animals existing on a fractal surface should have body masses that reflect that complexity. Using this interpretation, the species:body length distributions should have a slope somewhere between -1.5 and -3.0 . This interpretation has since been endorsed by May (1986).

Lawton (1986) considered that the standard relationship between numbers of individuals and number of species, defined by the log-normal distribution (see May,

1978, 1981) is approximately $S \sim N^{0.25}$, and that this would imply a $1780^{0.25}$ -fold increase in the number of species for an order of magnitude reduction in body length, if the underlying distribution of species abundances is log-normal for species of different body sizes. However, the predicted value was only 6.5, which is not big enough to account for observed increases in the number of species. But if one considered the habitat surface to be fractal, then decreasing the body size of the animals would result in the measured available space being even larger. More space could allow for more species, which could account for the seemingly disproportionate increase in the number of species following a decrease in body length.

Morse *et al.* (1988) proposed that all of the distributions are in fact related. A three-dimensional plot of log abundance per species versus number of species versus log body size class revealed a relatively simple smooth surface, at least for the beetle community of Bornean tree canopies. Results were presented without much description and no comparisons were made between tree species, disallowing any comparisons to changes in plant complexity. In contrast to the smooth shape of the data from the Bornean tree canopies, Basset and Kitching (1991) found that the three-dimensional plot of Australian rainforest tree species had a much rougher shape than the Bornean data with sharp differences between size abundance classes. The Australian study involved daily sampling over two years, which the authors thought could emphasize and alter the number of species per log abundance classes. A sub sample of the first four weeks of the study produced a noticeably smoother curve.

Clumps

The Holling school of thought sees the habitat as a self-organizing structure driven by a hierarchical set of simultaneously operating processes affecting scale specific

features (Holling 1986). An example from Holling *et al.* (1996) illustrates this point for a forest ecosystem. Small fast processes such as soil and plant physiological processes affect structure at scales of a single leaf to the whole plant. Slower processes such as competition for light and nutrient affect structure at the scale of a patch or gap. The even slower processes of fire, wind, insect outbreak and large mammal herbivory affect structure at the scale of a whole forest stand. The slowest geological and climatic processes affect landscape level structures. One may quibble about rates and scales or whether there is overlap between processes, but overall, this way of looking at an ecosystem provides a useful framework for understanding the hierarchical of structure in the habitat. The extrapolation of Holling's model is that since these processes are disjunct and operating at specific scales, the end result is an ecosystem organized in a 'lumpy' manner.

Kolasa (1989) investigated the idea that if the environment were hierarchical in structure, then clumps of animal abundances should occur at the distinct levels of recognizable sub-units. In general, any hierarchical system can be divided into smaller portions of distinct structure. If a particular organism is specialized to using only that sub-unit, then it will only be found there and will occur in lower numbers than a generalist occupying the entire area. All things being equal, the abundance of the specialist relative to the generalist will reflect the relative size of the specialist's sub-unit to the entire habitat. If one considers that there are a discrete number of identifiable levels in which a habitat can be divided, then a list of the abundance of organisms should show clusters of species corresponding to those levels. Kolasa (1989) supports this idea with a list of the number of habitats occupied by species of *Turbellaria* in an Italian

stream. Species could occupy anywhere from one to 34 microhabitats within the stream, but some broad ranges of the potential space were not represented by the data.

The concept of a lumpy environment may be self-evident, but the linking of process to structure was a conceptual leap. Furthermore, since these processes are operating at different time intervals, then the resulting structures will have a renewal rate (or persistence) comparable to the size of the structures. If this is the case, then Holling maintains that patterns in the behavioral and morphological attributes of the animal communities will reflect the patterns observed in the environment (Holling 1992; and Holling *et al.* 1996). Specifically, he considered the mean adult body mass of an animal to be a fundamental measure of how a given species perceives and utilizes the resources within a given ecosystem. In essence, large animals view the environment at a coarse grain while small animals view the environment at a fine grain. At risk of oversimplification, the assumption can be restated as saying that small animals can survive on small patches of food but cannot travel far, while large animals need larger patches of food but can travel further to reach them. If the distribution of resources is fractal, then not all animals will perceive the lumpy distribution of resources in the same manner. Rather, accessible resources will vary continuously with changes in an animal's body mass. The end result should be that there would be a greater richness of species at those body masses that perceive a greater amount of resources in that particular habitat. The lumpiness of the habitat should be reflected in the distribution of mean adult body masses of the animals occupying it.

The paradigm here is that physical attributes of the animal community (e.g., body size) are an echo of the physical structure of the environment. Holling and his co-

workers have produced an extensive body of work suggesting that body masses of animal species are arranged in clumps, the overall pattern of which appears to remain similar for similar types of habitat. For example, adult body mass of birds and mammals in boreal biomes of North America fall into distinct clumps, the distribution of which depends on whether one is considering forest, prairie, or aquatic ecosystems (Holling 1992).

Numerous techniques exist for analyzing structure in a distribution of adult animal masses. In general, the values are ranked from lowest to highest, and then a statistic is applied to the data to find gaps or clumps. A gap-detecting statistic developed by Holling (1992) is the Body Mass Difference Index, which in later papers is called the Size Difference Index (Holling *et al.* 1996). The index is arrived at using the following equation.

$$SDI = \left(\frac{S_{i+1} - S_{i-1}}{S_i} \right)^{\gamma}$$

where S_i is the body mass of the i th species in ascending size rank order and γ is a de-trending exponent. Values for γ were 1.3 for boreal bird data and 1.1 for mammal data (Holling 1992). A plot of the SDI as a function of the size order results in a graph where high values represent species that are relatively isolated with regards to their body mass. Low values on the plot can be thought of as clumps of species with similar body masses. Holling (1992) arbitrarily defined a clump as at least two consecutive SDI values exceeding the mean plus 2 standard errors, followed by at least four values below that. Once the clumps are identified, we can determine what proportion of species occurs in that clump and over what size range the clumps occur. It is then possible to compare different ecosystems by plotting these values for each clump.

Although there does not seem to be a means of attributing a given gap or clump to a specific feature of the environment, it does appear that similar habitats have similar distributions of gaps and clumps. To date, these body mass patterns have only been compared to habitat complexity in a qualitative manner. It is assumed that grasslands are simpler than tropical rainforests, with temperate forests lying somewhere between. Qualitative evaluation of the pattern of clumps and gaps does appear to remain consistent for habitats of similar complexity. This begs the question as to why should the distribution of animal body masses reflect the complexity of the environment. Holling *et al.* (1996) touch briefly on this. They suggest that gaps in body masses represent "forbidden zones of landscape scale" where the resources are insufficient for utilization by animals of those body sizes. Animals that are smaller would be capable of utilizing resources on a finer scale and animals that are larger could utilize resources on larger scales. The implication is that animals feed at particular scales and that there is a one to one relationship between body mass gaps and features of the environment.

Predator Effect on Community Shape

It seems simplistic, on the verge of being banal, to say that predators affect the prey community. It seems straightforward to take an aquarium fish and feed it certain types of prey items and measure the impact. But the natural world has a great number of additional variables that can complicate this relationship. Neither prey nor predator are confined to a single area but are free to travel to new areas and new patches of food. In addition, there are more than one kind of predator seeking each potential prey item and usually more than one kind of potential prey item for any given predator. The dynamics can be complicated and the effects are not always easy to measure. The effects a given

predator has on a community can be divided into those that directly impact a given prey species and those that are indirectly impacted by the direct effect on the prey species. These latter effects are sometimes called "cascade effects".

Direct effects

Predators have been found capable of eliminating a species from a given habitat (Brooks and Dodson 1965; Dodson 1970; and Sprules 1972). Most often, this effect comes from an increase in predation intensity lowering the overall prey biomass and resulting in a corresponding decrease in prey species richness. This has been found to be the case for aquatic habitats (e.g., bluegill introduced into ponds (Crowder and Cooper 1982)), as well as terrestrial habitats (e.g., spiders in a field enclosure (Provencher and Riechert 1994)). The effect may also result from a behavioral change in the prey. DeVries (1990) found that bluegill optimally feed in the deeper waters and preferred to be there, but when largemouth bass are present, the bluegill hide in the shallow vegetated areas. If the vegetation is removed, they still spend more time in the shallows. Giving the largemouth bass an alternate and larger prey item was not enough to lure the bluegill back to their optimal feeding areas. The presence of the predator eliminated the bluegill from deep-water habitats as effectively as if they had all been eaten

But adding or increasing the density of a predator does not usually result in a simple, linear change to the prey. Numerous interactions are possible often resulting in unexpected changes. A pair of studies examined the effects of generalist predators on terrestrial arthropod communities (Hurd and Eisenberg 1990; Fagan and Hurd 1991). They elevated the densities of either a mantid species, *Mantis religiosa* L., or an assemblage of cursorial spiders inside field cages. The mantids reduced biomass almost exclusively by reducing the number of grasshoppers and crickets (i.e., large predators

consumed the large prey). The spiders also reduced the grasshoppers, but unexplainably, the crickets increased in number resulting in no net change in biomass.

Barkai and McQuaid (1988) found an ecosystem with two stable states each driven by predation. At one island near South Africa, rock lobsters and seaweed dominate. The lobsters remove mussels and whelks but cannot eliminate them. At another island, the rock lobsters had been removed (for an unknown reason). Mussels now dominate the area and whelks are so numerous that they can overwhelm and eat any lobsters transplanted into the area.

Often there is only indirect evidence that predation is structuring the community. Rodríguez and Lewis (1997) examined the fish communities of 20 lakes in the Orinoco floodplains of Venezuela. They attempted to find correlations between fish assemblage and 22 different environmental variables. Only four of the 22 variables could reliably predict fish assemblage structure. These were transparency, conductance, depth, and area. Depth and area are causal to transparency while conductance was incidentally important because of biogeographic correlations. Transparency stood alone as a prime-structuring variable. The authors attribute transparency's impact on visual predators as the structuring force. Both clear and turbid waters had predators and had similar densities of fish but each supported its own suite of fish species. The implication is that clear water selects for fish with good eyesight because either good vision allows one to be a more efficient predator or it makes it easier to spot an attacking predator.

Paine (1966) hypothesized that rather than eliminating species, a predator could increase the diversity of species present by preventing any one species from monopolizing the habitat. Such predators were termed as "keystone predators" in the

sense that their removal would cause the structure to collapse. Murdoch (1969) maintained that predation could be a stabilizing force on two competing species provided that the predator did not have a constant preference for either species. If the predator was "switching" in the classic optimum feeding manner, then two or more competing species could more easily coexist, resulting in increased diversity. Addicott (1974) sought to test this proposed increase in diversity. He examined the effect of a mosquito larva, *Wyeomia smithii* (Coq.), as predators of ciliated and flagellated protozoans as well as of rotifers, had on the community structure of water filled pitchers of the northern pitcher plant *Sarracenia purpurea* L. While the micro communities did become more even in relative abundance, the overall number of species present decreased under predation.

Virnstein (1977) considered the effect of three different predators on the infauna of Chesapeake Bay. Two fish species and a crab species were either excluded from or confined to an area enclosed by a wire cage. Excluding these predators led to large increases in density and diversity. Most of this effect came from the opportunistic (i.e. weed) species with planktonic larvae and rapid growth. Confining fish to the cages resulted in slight decreases in diversity. The assumption was that natural predation pressure was extreme and that resources are not limiting. If increasing predation pressure had resulted in increased diversity, then one could have assumed that competitive interactions dominated this system.

In situations where competition between prey species is high, predators clearly do allow coexistence. Russ (1980) excluded grazing fish from substrates dominated by sessile marine invertebrates. Without this predatory grazing, the invertebrates competed for space and the substrate was eventually dominated by only one species. With fish

allowed access, competition had minimal effect and resulted in significantly higher diversity albeit a significantly lower standing crop.

Worthen (1989) examined three species of *Drosophila* that were reared together on commercial mushrooms. A predatory staphylinid was reared with half the replicates. If the predator was present, then all three species of fly could coexist. If the predator was excluded, then production of all fly species was reduced and one species, *D. tripunctata* Loew, dominated the other two to the point where they were often excluded. Worthen *et al.* (1996) found similar results in wild conditions when they were studying the nested distribution of mycophagous flies colonizing mushrooms. As an aside, they noticed that if ants had access to the mushrooms, then the fly community thereon was more diverse. If the ants were excluded, fly diversity dropped.

One of the most precise experiments to measure the effect of predation was performed by Thorp and Cothran (1984). They submerged screened trays filled with 2 cm of sediment from the surrounding area. The sediment had been filtered of all large predators and seeded with 0, 2, 4 or 8 large odonate nymphs. Overall, there was a small but significant effect on richness with a third order polynomial offering the best visual fit to the data. In other words, medium levels of predation resulted in the richest communities. Measures of evenness and diversity (i.e., Shannon-Wiener) were linearly related to predation intensity.

Aside from changes to the diversity and richness of the prey community, predation has been known to skew the size distribution of the prey. This has been especially well documented in aquatic systems, where the reduction in number of large prey items has been noted for a wide range of prey types. Galbraith (1967) noted this

impact on *Daphnia* spp. populations and Parker (1971) measured this impact on salmonid fishes. This effect was especially well documented by Crowder and Cooper (1982) who introduced bluegill into experimental ponds. They noted an overall decrease in prey biomass accompanied by an overall decrease in the mean prey size.

Predation can be so intense as to eliminate large prey from the habitat. Brooks and Dodson (1965) found that planktivorous fish could eliminate all large species of plankton from a lake. This impact can be geographically precise in action. Sprules (1972) found that in high altitude pools, the two main predators survived in large pools, but that the winter freezes excluded them from small pools. A comparison of the prey species found that small pools were dominated by larger congeners, while the smaller congeners dominated the large pools. This occurred even if the pools were side by side.

This impact is not always so neat and obvious. Zaret (1980) described two kinds of predators with differing effect on the prey population. One was gape-limited and swallowed its prey whole, but was fully capable of handling all zooplankton. This type of predator quickly eliminated large prey species and shifted the entire prey size-frequency towards the smaller species. The other kind of predator took bites out of its prey and was limited not by how much it can swallow but by how easily it could handle its prey. Prey could escape these predators by outgrowing them or by developing physical structures to hinder predators. The end result is that the prey population suffers a reduction in medium sized prey and an increase in spines or other armature.

Brett (1992) documented a similar effect under laboratory conditions. Cultures of *Daphnia* were subjected to either *Chaoborus* larvae or a simulated fish predation. The fly larvae found it difficult to successfully attack the largest *Daphnia*. Fish are known to

attack the largest *Daphnia* available and so sweeping a net of appropriate mesh size, through the water mimicked fish predation. *Chaoborus* predation led to increased average size of the *Daphnia* and the growth of defensive structures. The simulated fish predation resulted in a smaller average size of the *Daphnia* with no increase in defensive structures.

As with all complex systems, the interplay of factors sometimes results in an effect that is directly opposite to that which is expected. Such was the case with a study that found that removing predators from a system resulted in a decrease in the mean prey size (Persson *et al.* 1996). Northern pike were removed from two lakes and left alone in two other comparable lakes. If the northern pike were absent then yellow perch, *Perca flavescens* (Mitchill), were present throughout the lake. This resulted in slow growth, presumably because the yellow perch were resource limited. If northern pike were present, then yellow perch tended to remain in the littoral zone and their adult growth was faster. While this is still a direct effect of the northern pike on the yellow perch, this type of convoluted interaction is more typical of the indirect effects covered in the next section.

Direct predation effects become even more complicated when there are two or more prey species in potential competition with each other. Lynch (1977) held that each potential prey species had a feeding efficiency that was a function of its body size. Larger sizes are more efficient feeders up to a limit. In addition, each prey species has a vulnerability to predation, which is also a function of its body size, larger being more vulnerable. Overall fitness should therefore be a product of these two functions. The

implication is that for any given species in a particular situation, there will be an optimum body size.

Holt (1984) developed an interesting model based on these assumptions. If we assume multiple prey species undergoing logistic growth in a homogenous environment, then an apparent competition would develop between the species in regards to their vulnerability to the predator. A given prey species could exist within a community if its sensitivity to predation was no higher than the average sensitivity to predation of the whole community divided by a measure of the intensity of predation. In other words, if predation pressure was high, then all co-existing species needed to have similar sensitivities to predation, or the ones with higher sensitivities would be eliminated.

The implication is that if one species can out compete another for food resources, then that second species needs to be a lot less susceptible to predation in order to coexist. Schoener (1968) examined competition between lizard species. The island of South Bimini contains four species of lizard of the genus *Anolis*. These species can all co-occur on the same horizontal patch of land but divide the habitat up vertically. The species that overlap the most are most divergent in size.

Evidence that predation is responsible for divergent body sizes was produced by Juliano and Lawton (1990a, b). They took linear measurements of dytiscid beetles along several axes and then used these measurements to analyze body mass distributions in several streams. Seven sites were small, acidic, and lacked fish. In these sites there was little evidence for widely or regularly spaced body forms. Two sites were large, buffered and contained fish. In these sites there was significantly wider and more regular dispersion of body forms. This pattern could not be attributed to competition since the

beetles were not food limited. However, they did not consider any factors other than competition or predation.

Cascade effects

Cascade effects, often called trophic cascade or just plain indirect effects, are poorly understood but increasingly well documented. In simple terms, a cascade effect is when one species is impacted indirectly by the predator's actions. The simplest of these is the impact predation has on vegetation by reducing the number of herbivores.

Blaustein *et al.* (1995) found that the hemipteran predator, *Notonecta maculata* Fabricius, could eliminate a mosquito, *Culiseta longiareolata* (Macquart), in desert pools resulting in increased periphyton. Equally simple is the impact predators can have on non-prey animals by eliminating their predators. Crowder and Cooper (1982) introduced bluegill into ponds. This resulted in more midges and caenid mayflies present because bluegill eliminated their large invertebrate predators. Cascades have been noted in terrestrial habitats as well. Fagan and Hurd (1994) added mantid egg cases to old-field plots surrounded with sticky-trap dispersal barriers. Numbers and biomass of other arthropods generally declined but some species increased. Specifically, the number of hemipterans increased as a result of their predators being reduced.

These types of effects can oscillate through several trophic levels. Martin *et al.* (1992) noted a fish driven trophic cascade in the littoral community of freshwater lakes. Excluding fish led to increases in the snail population, which lead to decreases in the periphyton and increases in the macrophytes. Enhancing fish populations lead to decreases in the snail population, which lead to increased periphyton and decreases in the macrophytes.

The impact can still be significant even if the prey is not eliminated. Moran *et al.* (1996) noted a significant cascade when mantid egg cases were added to old-field plots. Including mantids led to an increase in spider emigration from plots. Herbivore abundance did not change, but their size distribution became skewed to the smaller species, which resulted in decreased total herbivore biomass. Plant biomass was 30% greater in plots with mantids.

Turner and Mittelbach (1990) added small bluegill to all of their experimental ponds and largemouth bass to only some of the ponds. Few bluegill were actually eaten by the largemouth bass and the bluegill density remained roughly equal in all ponds. However, when largemouth bass were present, the bluegill tended to avoid the open water and inhabited the vegetated areas of the ponds. This resulted in large increases in the number of zooplankton. In effect, the largemouth bass created a mid-water refuge for zooplankton.

Indirect effects may be as important as direct disturbance. Menge (1995) examined marine rocky intertidal interaction webs and found that indirect effects accounted for about 40% of the change in community structure. The proportion of change due to indirect effects was constant with web species richness, indicating that strong direct interaction and indirect effects produce roughly the same level of alteration of community structure regardless of the level of web complexity. With increasing web diversity, each species interacted strongly with more species, was involved in more indirect effects, and was part of more interaction pathways.

The entire concept of cascades is intimately tied to the contentious notion that animal population levels are controlled by top-down forces (i.e., predation) rather than

bottom-up forces (i.e., resource limited). Hairston *et al.* (1960) came up with the concept that "the world is green", therefore all herbivores are not limited by resources but rather are controlled by predation. There are plenty of exceptions where the habitat may be green, but the animals are still food limited. These exceptions tend to illustrate interesting biological concepts. Examples include the study of plant defenses and the specialization into micro-niches.

It is also readily apparent that the world is not green everywhere, but in some places the plant communities are eaten away to almost nothing. Fretwell (1977, 1987) suggested that the determining factor, as to whether the herbivores are controlled by predators or resource limited, lies in the number of trophic levels in operation. The top trophic level is always resource limited since by definition the top trophic level is not fed on by anything. The trophic level immediately below the top is controlled by the top trophic level and is not resource limited. This in turn means that the trophic level below that one does not suffer much predation and is resource limited. To summarize, the top trophic level and every second level below it are resource limited. The penultimate trophic level and every second level below it are controlled by predation. The implication is that an odd number of trophic levels results in a green habitat, while an even number of trophic levels results in a barren habitat.

If this is correct, then cascades work by adding or subtracting a trophic level. Power (1992) in an excellent review on the whole subject, supported Fretwell's concepts but cautions the obvious problems in identifying and delineating the number of trophic levels. She also stresses the idea that increasing the productivity in an area will sequentially add trophic levels.

Not all cascades have a trophic origin. Flecker (1992) found that insectivorous fish had a weak effect on the overall population levels of the invertebrate fauna of freshwater streams. This is not surprising given that the stream represents constant recruitment from upstream areas already impacted by insectivorous fish. Detritivore and grazing fish significantly reduced the population levels of all taxa. This was partly due to physical disturbance of the sediment and its removal by the current since mechanically removing the sediment led to similar reductions in some of the invertebrate taxa. But much of the effect was presumably that invertebrates could be intimidated into leaving the area by the actions of a grazing fish.

Abiotic cascades had been noted before. Vanni and Findlay (1990) found that while both yellow perch, and dipteran larvae of the genus *Chaoborus* caused similar reductions in size and biomass of the zooplankton community, they caused different responses in the phytoplankton. Yellow perch caused large increases in the algae communities. This cascade was not due to a reduction in zooplankton grazing but rather the fish caused more rapid cycling of the phosphorus in the water column leading to the algae bloom.

Predation as a Constant Force

There are numerous reports in the literature of a change in a predator species having a measurable impact on the prey community. Curiously, there are also reports where a change in the predator had little or no impact on the prey community. Young and Young (1978) used cages to enclose or exclude predatory fish on patches of seagrass, *Halodule wrightii* Ascherson. Enclosing a predator inside the cage had no effect on macrobenthic densities. If fish were excluded from the cage, only some of the species would increase in density. Clipping the seagrass had a much more dramatic impact with

some species increasing and some species decreasing in number. Their assumption was that relative importance of predation must have been differing for each of the 11 species selected.

Several cage exclusion/inclusion studies followed that had similar results. Gilinsky (1984) stocked submerged cages with three different densities of bluegill. Some species were significantly impacted by fish predation, but fish densities had no effect on most groups. He concluded that bluegill are not keystone predators and have little effect on structuring the pond littoral community. Bell (1985) placed polychaete tube-caps out in the shallow sand flats of Tampa Bay and examined the meiofauna that colonized them. High complexity tube-caps did have higher abundance of meiofauna, but predator exclusion cages did not affect the results. Webb and Parsons (1991) excluded predators from cages inside seagrass meadows and then sampled the substrate for copepods. They found no effect and attributed this to the seagrass, which offered a good refuge. That is, if the predators already have a hard time getting in because of the seagrass, then there will be little effect demonstrated in excluding them.

These authors are probably correct in their assumptions as to why their particular predators had little or no effect on the prey community. But these varied explanations may be only part of the explanation. The fish that were being excluded represent one kind of predator. A whole suite of predator species attacks any given prey community. Each predator species will preferentially attack and consume part of that prey community. If predators exploit potential prey yet avoid competition, then changing one member of the suite will cause other members of the suite to compensate. The result is

that predation can be thought of as a force independent of the taxonomic makeup of the predators.

A fish, *Perca flavescens*, and a fly larva of the genus *Chaoborus* both caused similar reductions in size and biomass of the zooplankton community (Vanni and Findlay 1990). Consider also that total mortality inflicted by all predators on velvetbean caterpillars, *Anticarsia gemmatilis* (Huebner), was the same for predator complexes with different species composition (Elvin *et al.* 1983; and O'Neil and Stimac 1988a, b). Finally, consider that four different species of coccinellid beetle with large differences in foraging behavior had similar effectiveness while foraging for aphids on different varieties of plants (Grevstad and Klepetka 1992).

In order for this to work, predators need to divide up the prey resource in a manner that minimizes competition. Wilson (1975) noted that different sized animals eat different sized prey so they could reduce competition. The limits in prey size for a given predator may be based on physical attributes of the predator. Murakami (1983) showed that an orb-web spider, *Argiope amoena* L. Koch, had an upper limit of prey size that was equal to the distance between the first and third legs of the spider. Its lower limit of prey size was any prey that could pass straight through the web.

Tadpole shrimp feed on mosquito larvae in a size selective fashion (Tietze and Mulla 1989). Small shrimp feed preferentially on 2nd instar mosquito larvae. As the shrimp increase in size, the bias against large larvae decreases. The largest shrimps show no size preference. This was apparently due solely to the limits in the ability of the shrimp to hold and subdue their prey.

Size selection by predators may be based on optimal foraging choices made by the predator. Small specimens of a freshwater planktivorous fish, *Xenomelaniris venezuelae* (L.), selected rotifers (Unger and Lewis 1983). Larger fish selected successively larger prey items with diet breadth inversely related to fish size (i.e., larger fish were more selective in their diets). The authors attribute this to increased capture efficiency and growth-related improvements in vision. Paulissen (1987) found that the most profitable prey items for large racerunner lizards, *Cnemidophorus* spp., were various grasshoppers. For smaller lizards, smaller and less active prey were the most profitable. Their foraging behavior reflected these calculated benefits. Large lizards move rapidly through an area, while smaller lizards searched the vegetation slowly and diligently.

Energetic arguments along the line of optimal foraging imply that small predators eat smaller prey because the handling costs of eating large prey outweigh the benefit, whereas for large predators, the additional costs are minimal and large prey are optimum (Griffiths 1980). If on the other hand, predator size influences predator foraging behavior, then this could result in different sized prey items being encountered (Huey and Pianka 1981; Price 1983; Paulissen 1987; and Read 1984). Beetle larvae, *Dytiscus verticalis* Say, hunting tadpoles, had a greater reaction distance for larger instars (Formanowicz 1987). The area of the swath was greater for larger larvae as well

Dividing up the prey community on the basis of size is not the only way that predators minimize competition. They can also hunt in specific places. Anthocorid predators spend a lot of time searching midribs and edges of leaves (Evans 1976b). These are the areas where their aphid prey are most likely to be. A parasitic wasp

searching for aphid hosts on wheat would search each leaf equally, but the ear of the plant was searched less often (Gardner and Dixon 1985). Aphids on the ear were somewhat protected from attack by the seeds. Northern goshawks, *Accipiter gentiles* (L.), hunted in areas of a particular forest structure. They preferred areas that had higher canopy closure, greater tree density, and greater density of large trees (Beier and Drennan 1997). Fish too, can preferentially feed in specific areas. Smith and Coull (1982) found that juvenile *Leiostomus xanthurus* preferentially fed on mud substrate rather than sand areas. If given no choice, these fish would feed on meiofauna from either area. For all of these predators, any prey items that were not in the areas that these particular predators searched would be available for different predators to attack.

One of the best studies to show that predators divide up the available resources based on differences of scale was done by Roland and Taylor (1997). They examined the pupal weights of different fly parasitoids and tried to correlate these with their prey, the forest tent caterpillar, *Malacosoma disstria* Hubner. To do this, they analyzed forest structure (forested vs. cleared) across numerous scales and then tried to find at which scales the different fly parasitoids showed maximum correlation to the frequency of their caterpillar prey. Their results, summarized in Table 12, show that the parasitoids are exploiting the caterpillars in a scale specific matter that seems to be keyed into changes in the forest structure. The authors thought that this correlation was due to the size of the parasitoid being linked to its flying distance.

So if size selective division of prey is a wide spread phenomenon, then what effect would this have on prey populations? The simplest response is for prey to show size specific mortalities when attacked by single predators. Collembola have been found

to suffer size specific mortalities (Straalen 1985). Two species were found to suffer disproportionately high mortality in the early instars due to the predatory actions of a staphylinid beetle. This type of predation can lead to size specific changes in prey behavior. Tolan *et al.* (1997) examined the distribution of larval and juvenile fishes in seagrass beds off the coast of southern Texas. Early larvae showed no correlation with any type of seagrass, even versus open waters. The presence of larger juveniles was highly correlated with vegetation, especially with *Halodule wrightii*, whose beds were measured as being the densest of all.

Table 12. Correlations between fly parasitoids and caterpillar prey in Alberta forests (Roland and Taylor 1997).

Parasitoid	Pupal size (mg)	Forest scale of max correlation (m)
<i>Carcelia malcosomae</i>	34	53
<i>Patelloa pachypyga</i>	41	212
<i>Arachnidomyia aldrichi</i>	58	425
<i>Lescheaultia exul</i>	68	850

Interestingly, these size specific responses do not seem to always work when a cage is used to isolate or exclude predators on a patch. Nelson (1979) found that when fish were enclosed on a patch of eelgrass, *Zostera marina* L., then numbers of amphipods decreased from the increase in localized predation and some species disappeared. If fish were excluded from a section of the eelgrass beds, then amphipod density, richness, diversity, and evenness were not significantly different from uncaged areas of eelgrass. Apparently, decapod predation increased in the absence of fish resulting in no net change in the amphipod community. Thorp and Bergey (1981) placed cages that excluded fish

and turtles in the littoral zone of a soft-bottom reservoir. They found a slight tendency for invertebrate predators to increase when vertebrates were excluded, but in general, there was little effect. There was a significant trend for most functional groups to be reduced within the cages and a few taxa were eliminated when vertebrates were excluded, but other taxa increased to make up the difference.

This cannot be written off as just a cage effect in that it has also been shown to occur when new predators are introduced into pools. Diehl (1992) found an excellent example of one predator replacing another with no resulting changes in the prey. Yellow perch, an omnivore, was introduced into vegetated and unvegetated ponds. The biomass of predatory invertebrates was reduced, but herbivorous invertebrates were unaffected.

This compensation of one size class of predator making up for a missing size class of predator has also been reported in terrestrial habitats. Dickman (1988) examined the relationship between body size and prey size in three two-species communities of insectivorous mammals in Australia and England. He found that in the lab, all insectivores preferred the larger insects and that even the largest invertebrates posed insignificant energetic demands on the smallest predators. In the wild, larger predators dug deeper into the soil and searched thicker clumps of vegetation than smaller predators and so encountered larger prey items. If the large predators were excluded, then the smaller predators began to hunt the more profitable areas and eat larger prey items.

Compensation is not a one-way street. Changes in the prey community can also impact the predator guild. When mantid egg cases were added to an old-field site, their hatch resulted in a sudden increase in the density of predators (Moran and Hurd 1994).

The resulting higher levels of intra-guild competition caused predators of all species to emigrate or die off resulting in little overall change in predation levels.

The adjustment of predators to the levels of prey seems to be a universal phenomenon. Winemiller and Pianka (1990) found it to occur in desert lizard communities as well as tropical fish assemblages. If the number of predator species was low, then there was broad dietary overlap among the predators. If the number of predator species was high, then the predators began to show strong resource partitioning. They divided the resource and concentrated on separate groups of prey species. When the number of prey types was low (i.e., 19 prey types), then predators showed strong guild structure and concentrated on a few of the available prey species. When the number of prey types was high (i.e., more than 200 prey types), division of food resources disappeared and the predators showed spatial niche segregation.

If the type of predators is diverse in either species content or size class, then the predator suite will share the prey between the types resulting in the prey community being divided up by size class. A concentration of the predator effort over a few size classes of prey results in size specific mortality rates in the prey leading to peaks in prey number not in those size classes. In contrast, a high degree of variation in the predators diffuses the predation effort over many prey size classes resulting in a more even distribution of prey sizes. A community with a diverse array of predators can be thought of as being saturated and relatively stable in the face of a change in some of the predators.

There is some evidence that this type of saturation occurs. Pitfall traps revealed that the size range of spiders parallels that of the potential prey items (Nentwig 1982). This means that spiders always exerted optimal predation pressure on all size classes of

potential prey items. The cage exclusion/inclusion experiments discussed above also support the idea that predation can be diffused across a suite of predators rather than being concentrated in one key predator. Chilton and Margraf (1990) used cages to either exclude or enclose fish in *Vallisneria* beds. There was an overall increase in the abundance of invertebrates within the cages, and the size distribution of the invertebrates changed. Inside each cage there was an increase in the number of large primarily predatory invertebrates and a subsequent drop in small immobile invertebrates. Furthermore, there was no significant difference between cages with all fish excluded and those cages with a 70-mm bluegill enclosed. The implication is that one bluegill is roughly equivalent to the predatory invertebrates. What the cages really did was size limit predation so that it was possible to outgrow the predators and escape predation within the cages.

Arena Affect on Community Shape

While predation definitely has an impact on the community's shape, it does not do so in isolation. The structure of the arena also impacts on this shape. Whether it is by physical protection, the providing of food, or a complex behavioral mechanism, structure in the habitat unarguably tends to increase biomass of the fauna. How it does this is mostly unknown and how the increased biomass is distributed in the community is complicated and essentially unpredictable. What is known, is that the parts of structure that influence the community can be divided into three types. While the literature commonly fails to distinguish them, the three types are amount of structure (density), the variety of structure (heterogeneity), and the form of structure (complexity). Increasing the amount of structure, also called density, is here defined as increasing the number of

objects in the arena. Increasing the variety of structure, also called heterogeneity, is here defined as increasing the number of types of objects in the arena. Increasing the complexity of the arena is here defined as altering the form of the objects in such a manner as to increase the apparent dimension. While often compounded, it is possible to change each of these factors independently.

Amount of Structure

It has long been realized that increasing the amount of structure in an area will lead to an increase in the number of animals occupying that area. The details of this effect on the community other than changing the abundance are less well understood. Heck and Wetstone (1977) examined the macroinvertebrate fauna of Panama seagrass beds, *Thalassia testudinum* (König). They found that richness and abundance of these macroinvertebrates was significantly correlated with the above-substrate plant biomass of the beds. Animal richness was not related to plant richness, indicating the effect was due to the amount of structure in the environment. Woodin (1978) found that the tubes built by a polychaete worm were positively associated with increased abundance and richness of infauna in the immediate vicinity. This effect could be mimicked using drinking straws, showing that the effect is structural in nature. Angermeier and Schlosser (1989) suggested that for the fish community of two streams in each of Minnesota, Illinois, and Panama, species richness was best predicted by habitat volume. Their plot of the number of species versus the log volume of habitat still had a lot of scatter. The best fit for the relationship occurred in Panamanian streams and the worst in the Minnesotan waters. They speculated that harsh northern winters followed by a short reproductive window of variable success rate could lead to population instability, which keeps the community from achieving equilibrium status.

More recent studies have considered that correlations between the community and the amount of structure in the arena may be concentrated over specific scales. Rundle and Ormerod (1991) examined the microcrustacea in Welsh streams. They found that overall richness was highly correlated with percent coverage by macrophytes. Abundance showed no correlation except for the class Cladocera. Cladoceran abundance was highly correlated with macrophyte coverage and with substrate type. They were negatively correlated with boulders and cobbles but positively correlated with mud substrates. Note the change in scale involved with this. Downes *et al.* (1995) examined rock surfaces in Australian streams. There was an overall increase in number of species on stones having rough texture and high epilithon cover (i.e., increased structure). Faunal composition seemed to be linked to the abundance of the epilithon and weakly associated with large cavities of the rocks. Roundness of the rocks had no effect. Species richness was related with the number of small cavities.

Dibble *et al.* (1997) provide an excellent literature review on the general topic of how fish populations react to changes in aquatic macrophytes. They stress the importance of choosing the right scale to evaluate the effect of plants on fish. Most of the studies related to the response of a few species of fish at large scales. That is, entire fish populations were analyzed in response to patch sized changes in aquatic macrophytes. Behavioral data (i.e., small-scale interactions) were considered for only a few sunfish species with no real ability to extrapolate to large-scale population effects. They propose that this leap of predictive ability of population effects from behavioral data could occur through careful consideration of scale and plant structure.

The assumption in most of these studies is that predation is responsible for the correlations between structure and community. There is support for this assumption. Blaustein *et al.* (1995) found that *Notonecta maculata* in desert pools could eliminate *Culiseta longiareolata*. The predatory backswimmers had no significant effect on *Culex* and *Anopheles*, which had a strong positive association with surface vegetation. Woodin's (1978) study was followed up by a second study (Woodin 1981) in which she found that the increase in infaunal abundance of invertebrates as a function of the abundance of a polychaete worm was through the actions of predatory crabs. Excluding predatory crabs resulted in losing this correlation. In other words, the predators entrained the community around the structure of the tubeworms.

The relationship is not always that straightforward. Nelson (1979) found that the amphipod populations in eelgrass beds were strongly affected by predators. The two most abundant predators were the pinfish, *Lagodon rhomboids* (L.), and the grass shrimp, *Palaemonetes vulgaris* (Holthius). In his study, the structure of the arena was changed by increasing the number of blades in a bunch of seagrass, or by letting the amphipods build tubes. For shrimp predators, any blades present significantly increased prey survival in the short term. Over a longer time period (24 h), there was a general trend of decreased predation intensity with increased blade density although not all means were significant. For fish predators, blades did not produce much of a refuge. Higher densities of grass led to higher survival of prey, but differences were slight. Larger fish had less trouble finding prey in all cases. Allowing prey to construct tubes led to large increases in survival against all predators.

Orr and Resh (1991) found that *Anopheles* larvae survived in greater number if the density of *Myriophyllum aquaticum* was increased. While this difference was most dramatic when predatory mosquito fish were present, the effect still occurred when the fish were absent. This suggests an effect independent of predation, perhaps due to microclimate.

Variety of Structure

Even if the amount of structure is kept constant, there can still be a significant impact on the animal community from the way that that structure is situated in space. Here we consider how changing the variety of structure in the habitat impacts on the community. Variety, or heterogeneity, of structure is often confused with complexity. While they are related concepts in that heterogeneity requires changes in complexity, they are not the same. A uniform distribution of a complex type of object would have low heterogeneity.

MacArthur and MacArthur (1961) were among the first to consider changes of structure across space as a determinant of community structure. They coined the term foliage height diversity. They divided the height of plant communities into regions and determined leaf area along a vertical transect. They calculated an information index using the percent cover values for each of the regions. The resulting plot of bird species diversity versus foliage height diversity of deciduous forest plots revealed a positive straight-line relationship. MacArthur *et al.* (1962) found that when these layers were looked at independently, the percentage of leaves in different layers was a good predictor of breeding bird species.

Pianka (1966) also used a Shannon type information index, but he extended the comparisons into horizontal as well as vertical regions. He estimated the volume that

plants occupied by assuming them to be ovoid. Using these volumes, he calculated a plant volume diversity measure for ten different areas. The total number of lizard species in each of these areas showed a strong linear correlation to these volume diversity indices. Qualitative evaluation of the lizard species involved could link 10 of the 12 species to some particular structural aspect of the environment.

Clearly there is a relationship between the heterogeneity of an area and its animal community, but the effect seems to vary with species of animal. Kotzageorgis and Mason (1997) found that hedgerow structures affected small mammal populations, but that different aspects of structure affected different animal species. Groundcover, interconnectedness, and proximity to water each impacted on different species, and there was no apparent simple predictive response. These results mirror those of Rotenberry and Wiens (1980) who investigated the relationships between vegetation structure, spatial heterogeneity, and bird community structure in North American steppe vegetation. Individual species of birds were found most often in areas dominated by their preferred plant type, e.g., tallgrass prairie birds were most often found in areas dominated by grass and shrubsteppe birds had their highest abundances in areas dominated by shrubs. However, there was great variety in their response to spatial heterogeneity. The abundance of some species reacted positively to heterogeneity or patchiness, while others reacted negatively. The community was much more predictable. Overall diversity increased with increasing vertical heterogeneity, but varied independently of horizontal heterogeneity.

There have been fewer of these types of studies within the aquatic habitat and due to the inherent difficulty in measuring aquatic habitats, most of these studies suffer some

sort of problem. Scheffer *et al.* (1984) maintained that vegetation pattern is probably the main factor in determining spatial distribution of the non-benthic macro-invertebrates in a Dutch ditch. They really had no controls and no real explanation for why this should be. Benson and Magnuson (1992) found a strong correlation between habitat heterogeneity as measured using the Shannon-Weiner index, and the rarified species richness of Wisconsin freshwater fish from different lakes. Habitat heterogeneity was correlated with fish community heterogeneity between sites within the same lake, but was compounded with species of plant and depth diversity.

Questions on the impact of plant species differences rather than structural differences can also impact on terrestrial community studies. Rotenberry (1985) found that variation in bird communities from eight grassland habitats across central and western North America depended more on the species of plant involved rather than its structural shape. About 55% of the variation in the bird communities was attributable to plant taxonomy. Only 35% of the variation was attributable to plant physiognomy.

An alternative way to look at the habitat heterogeneity was developed by Haslett (1994). He considered that the patches of plant type in mountain meadows were essentially fractal in form. If one plotted these patches, their boundaries could be measured using box-counting. Increasing the number of patches within a meadow (i.e., increasing heterogeneity) led to more boundaries and a higher box-counting dimension. When he compared the populations of adult Syrphidae (Diptera) with the dimension of all patch boundaries, it was found that increased dimension resulted in increased diversity as well as an overall increase in density.

Form of Structure

Chapter 5 concerned the impact of form, measured as complexity, on the individual act of predation. Not surprisingly, form can have an impact on the whole animal community. In fact, structural complexity of a habitat is known to affect abundance, diversity, and distribution of its associated fauna (Huffaker 1958; and Cooper and Crowder 1979). The positive correlation between animals and structure in the environment has been studied numerous times and found to hold true for a great variety of animal taxa over a wide range of habitat types. It has been noted in birds (MacArthur and MacArthur 1961; MacArthur et al. 1962; Cody 1968; and MacArthur 1972), reptiles (Pianka 1966, 1973; and Schoener 1968), mammals (Simpson 1964), rodents (Rosenzweig and Winakur 1969), chydorid cladocerans (Whiteside and Harmsworth 1967), insects (Murdoch et al. 1972), and the faunas of caves (Poulson and Culver 1969).

The point is well illustrated by Quade (1969). He examined the Cladocera fauna associated with 12 different species of plants in seven lakes. Almost 3000 specimens belonging to 38 species were found and their grouping into different associations was evident. However, the grouping was not associated with lake, water condition, depth, temperature, or sediment type, but rather, the grouping seemed to be associated with plant growth form. These groupings are as follows: broad-leaved submersed plants, fine-leaved submersed plants, floating-leaved plants, as well as *Chara* sp. and *Nuphar variegatum* Engelmann as their own classes.

One of the first things noticed about the impact of form is that more complex shapes tend to support greater numbers of individuals. Kreeker (1939) was one of the first researchers to quantify the fauna on submerged vegetation. Many of the plants he examined are in this study. His sampling unit was 10 feet of plant material laid end to

end in a straight line. His results are present in Table 13. Note the strong correlation between complexity and the number of individuals.

Length of plant material is not a good way to compare different plant species. These plants vary in their widths and their leaf and branching patterns so that a given unit length would represent considerable differences in the amount of plant material. Rosine (1955) compared plants by looking at the abundance of animals versus the surface area of the plants. He measured the surface areas of three species of aquatic plants and counted the numbers of individual invertebrates thereon. He used a microscope and dividers to measure the plants at as fine a scale as possible and found consistent differences among the plants. Unfortunately, we are unable compare differences at the scale of the animals involved. However, his results for the average density of *Hyaella azteca* (Saussure) per 100 cm² of plant surface area do show a density response that parallels plant complexity (Table 14).

Table 13. Mean number of arthropods present on a standard length of aquatic plant material (Krecker 1939).

	# genera	# individuals/10feet
<i>Potamogeton compressus</i> L.	11	572
<i>P. pectinatus</i> L.	16	469
<i>P. crispus</i> L.	23	1139
<i>Myriophyllum spicatum</i> L.	23	1442
<i>Elodea canadensis</i> Michx.	26	564
<i>Najas flexilis</i> (Willd.) Ros. & Sch.	23	381
<i>Vallisneria spiralis</i> L.	5	30
TOTAL	29	4597

Table 14. Density of *Hyaella azteca* per 100 cm² of plant surface area (Rosine 1955).

Plant species	density (100 cm ⁻²)
<i>Chara delicatula</i> (Krause)	2
<i>Potamogeton gramineus</i> L.	1.3
<i>Polygonum natans</i> Eaton	0.3

Most studies look at the fauna on a given mass of plant material. Gerking (1957) sampled the fauna in and around *Elodea canadensis*, *Najas flexilis*, and *Vallisneria americana*. Many animal groups existed only on the plants and others only in the mud. Overall, *N. flexilis*, which has the most convoluted surface, supported the richest and densest populations of invertebrates. Gerking attributes this to the greater leaf area per mass of plant material. Benthos varied with root development. *V. americana* supported the greater benthic populations because of the extensive mass of its root system while *E. canadensis* had few roots and had the least benthos.

Surface area as the determining factor in animal abundance was supported by Lewis (1984). He found that thin bladed *Halodule wrightii* supported more individuals per unit biomass than wide leaved *Thalassia testudinum*. This came as a surprise to the researchers since they had assumed that wide leaved plants would offer better protection from predators. However, no mention was made of the size of the animals on these leaves.

Richness and diversity are certainly tied to the idea of abundance. Any increase in faunal abundance is sure to contain more rare species. However, there is also evidence that richness and diversity change along with changes in the structural form of the habitat even if abundance is kept constant. Talbot (1965) and Risk (1972) showed that topographically complex coral reef habitats support more fish species than simple ones

and that tropical marine predatory gastropods have more species in complex sub tidal reefs than lagoon sand and inter-bench habitats. Diversity of *Conus* gastropods as measured by Shannon H diversity indices correlates better with subjective measures of complexity (sand vs. limestone shelf vs. reef) than with either latitudinal gradients or distance from "center of dispersal" (Kohn 1967).

Rosenzweig and Winakur (1969) compared the density of granivorous, nocturnal desert rodents in Arizona with soil features (i.e., depth, texture, and resistance to sheer stress) as well as features of the vegetation (i.e., plant's species diversity, growth form, and foliage density). Significant variables were plant growth form and foliage density. They developed a Shannon type of information index derived from the foliage height diversity measure. There was good linear agreement between this complexity measure and the number of species coexisting in an area.

Abele (1974) performed a survey experiment that highlights this principle in a situation that is subjectively pleasing and easier to grasp for anyone familiar with seaside habitats. He sampled the decapod crustaceans from 10 marine habitats and then arranged them in what he subjectively determined was in order of increasing habitat complexity (Table 15). In general, the number of decapod species in a habitat seemed to correlate with habitat complexity.

Kohn and Leviten (1976) performed an experiment that helped to support the idea that this response was structural in nature. They examined assemblages of tropical inter-tidal predatory gastropods and found them to be affected by structure in a manner similar to the decapods discussed above. Both density and richness increased in the presence of structure. They took this study one step farther by adding artificial structure to the

environment and found that they could mimic the increase in density and richness in previously depauperate areas. Caley and St. John (1996) conducted a simpler experiment. The authors placed pipes in a marine habitat and thereby created artificial reefs. A loose screen, that allowed small fish to pass, was placed over one or both ends of the pipes. Both types of screening raised the richness and abundance of fishes on the reefs relative to unscreened pipes.

Table 15. Richness of decapod crustaceans sampled from increasingly complex marine habitats (Abele 1974).

Habitat	No. of Species
Temperate sandy beach	8
Tropical sand beach	7
Tropical sand-mud beach	16
Temperate <i>Spartina</i> marsh	14
Tropical rhizophora mangroves 1	17
Tropical rhizophora mangroves 2	20
Temperate man-made jetties	34
Tropical <i>Pocillopora</i> coral	55
Tropical rocky inter-tidal zone 1	67
Tropical rocky inter-tidal zone 2	78

These studies seem to indicate that the underlying community in a given type of environment had a predictable pattern dependent on the structure of the habitat. May (1981) termed this the "trophic skeleton" of the community. By this he meant that while individual species vary from site to site, species richness and diversity tend to remain constant and predictable if the environmental structure remained constant. In support of this contention he cites Simberloff and Wilson (in May 1981) where the fauna of small mangrove islets was eliminated and the re-colonization by terrestrial arthropods was studied. While the total number of species returned to normal, they were composed of a

different suite of species than what had been on the islands previously. In addition, all guilds were present in roughly the same proportions as before.

Recent work has concentrated on defining some of the species differences in a community's response to structure. Sometimes the species-specific impact of structure is fairly obvious. Spider communities in a salt marsh were affected by the structure of the vegetation (Döbel *et al.* 1990). *Spartina patens* Ait. Muhl. is a low matted plant that forms a dense thatch. These plants supported large numbers of hunting spiders, which had no difficulty moving through the thatch. *Spartina alternifolia* Loisel is a more erect plant with little thatch. These plants supported large numbers of web spinning spiders by providing many attachment sites.

Sometimes the relationship is not obvious or is hidden by some other factor. Species richness or overall abundance of gastropod species in the St. Lawrence River did not correlate with the presence of either of the plant species *Myriophyllum spicatum* or *Vallisneria americana* (Vincent *et al.* 1991). Only 3 of the 7 most abundant species of gastropod showed significant covariance with density of a particular plant species. Overall, the effect of plant species was weak compared to site and year. The authors suggested that the gastropods were calcium limited, and could not increase their number significantly.

Occasionally, a complex suite of factors is considered responsible for species-specific distributions. Evans and Norris (1997) took stereophotographs of stream bottoms and measured a number of different characteristics. Flow characteristics of the streams as well as physical characteristics of the stream bottom were considered, but no one characteristic could predict the presence of a given macroinvertebrate. A

combination of nine factors did result in reasonable success. They achieved 87% success in predicting the presence/absence of a macroinvertebrate that had >50% chance of being present and 93% accuracy for taxa with >70% chance of being present.

Given the number of individual species responses possible, it is pleasantly surprising to see a glimmer of order in the confusion. Such is the case of rank abundance graphs, where the species are arranged in decreasing order of abundance and plotted versus their actual abundances on a log-log plot. These types of studies often produce a relationship that correlates well with habitat structure.

Mason (1992) collected spiders from Douglas fir and true fir trees in three different habitat types in the Pacific Northwest. In each area, a rank abundance plot of the spider families produced a log-series that was different for each tree type. The author speculates that the familial structure of the spider community is determined by the branch and foliage characteristics of the trees. Further speculation was that if one examined the species within the families one might find the lognormal distribution postulated by May (1975). Unfortunately, this was not done.

Edgar (1994) used sieves to separate marine fauna into size classes. A linear negative relationship between log abundance and log sieve size was found on almost every habitat examined. The slope of this plot was related to habitat type and the absolute value of this slope could be taken as a measure of the size dominance of the fauna in a community. In other words, a low size dominance value indicated a more even distribution of the fauna over the size classes. A high size dominance value indicated that there were relatively few large animals and a great many small ones. Epifauna assemblages on detached macrophytes had extremely low size dominance values while

infaunal assemblages on seagrass beds had high values. Infaunal assemblages had higher size dominance than epifauna assemblages in all habitats examined. Overall, the trend was for epifauna size dominance to be higher in unvegetated habitats than in seagrass habitats, but little difference between seagrass types. Size dominance did vary significantly between epifauna assemblages on macro algae of different shapes. Assemblages on detached macro algae had the lowest size dominance values. There was little seasonal variation of size dominance on infaunal assemblages, but there was a general trend for epifauna assemblages to show a seasonal low in late spring and summer.

The constancy of this relationship was shown by Wolheim and Lovvorn (1996). They examined the invertebrate communities in Wyoming Saline lakes. They compared the invertebrate fauna on three growth forms of vegetation; thin-stemmed emergents, large submerged macrophytes, and low macro algae. While taxonomic composition and total abundance varied between lakes, the relative abundance of any given invertebrate species stayed constant when compared across plant growth forms.

Most of these studies are just concerned with describing the distribution without trying to attribute it to any particular cause. One notable exception is the work of Morse *et al.* (1988). They examined the arboreal beetle fauna from various trees in the Bornean rain forest. When the log total number of individuals (regardless of species) was plotted as a function of size class (classes were $5 * \log_e \text{ length}$), the resulting distribution had an upper tail with a near linear decline in log number of individuals with increasing size class. Furthermore, a linear equation fitted to the upper tail of the distribution had different slopes depending on whether one was plotting a particular guild of beetle or whether one was plotting all beetles off of different trees. Of particular interest was that

different tree species had differently shaped beetle communities. These trees were all part of the same forest and for the most part beetles were capable of migrating among tree species, yet something about the trees impacted the shape of the beetle community.

The work of Mittelbach (1981b) can be reconsidered in light of the paper by Morse *et al.* (1988). Mittelbach published data on the number of individual aquatic invertebrates per size class as a function of season. If these data are lumped into vegetated versus open sediment categories and plotted in a manner similar to that of Morse *et al.* (1988), we get the results shown in Figure 40. Note that both sediment and vegetation communities seem to be distributed in simple curvilinear relationships when examined on a log-log scale. The number of individuals per size classes for sediments peaks at greater abundance and a larger body size than for vegetation, but then drops off faster. Both distributions are much flatter than the beetle fauna examined by Morse *et al.* (1988), who suggested that the right side of the plot looks almost straight. These data suggest that their relationship could just as easily be interpreted as a parabola.

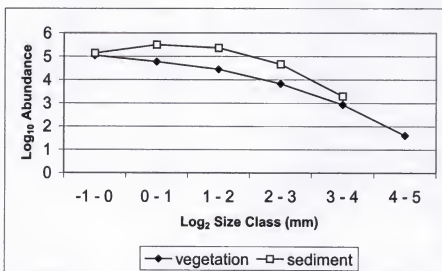


Figure 40. Abundance of aquatic arthropods relative to body size class based on data from Mittelbach (1981b).

Hanson (1990) measured the macro invertebrates from aquatic weed beds dominated by either the macro alga *Chara* or by rooted plants. He utilized the familiar $\log_2$ body size classes, but rather than show abundance per size class, he showed percent of total biomass in each size class. One could approximate the number of individuals by dividing the percent biomass by the mid value of the size class, but the actual numbers are unavailable and would have to be estimated from the graphs. The salient feature of his work is that the *Chara* plot is flatter, but both the *Chara* plot and the rooted plants plot tend to show bimodal peaks.

Peaks in any sort of abundance versus size plot imply that there are sizes of animal that are able to survive in the community in greater number. A possible explanation for this is if a particular sized structure in the habitat offers protection from predators, then an increase in that structure would result in increases in the number of animals capable of using that scale. This is reminiscent of the study of Downes *et al.* (1995), which was discussed earlier. Although there was no evidence that predators were responsible, they noticed a scale effect in the invertebrate response to structure. Invertebrates on stream rocks showed no correlation with the roundness of individual rocks, but species richness did show a strong response to cavities in the range of 0.36 mm or less. Additional support comes from the work of Choat and Ayling (1997). They found that intricate algae-dominated reefs supported larger numbers of small fish, while typically blocky coralline reefs supported greater numbers of big fish. This trend occurred across depth and temperature gradients, as well as across numerous different sampling scales.

Middleton et al. (1984) examined the fish community in beds of two species of seagrass, *Posidonia australis* Hook and *Zostera capricorni* Aschers., in Botany Bay, New South Wales. These two species formed structurally different beds. *P. australis* had much greater leaf length and width, and formed higher canopies. *Z. capricorni* leaves were thinner and formed denser mats. The fish fauna in the two beds showed no differences in heterogeneity, richness, total abundance, or Shannon-Weaver diversity indices. However, the size distribution of the fish peaked at small body sizes in the more open *Z. capricorni* beds as compared to the more enclosed *P. australis* beds. The authors suggested predator selection (Heck and Orth 1980) or active choice of the individual fish (Stoner 1980) as possible explanations.

Most of the evidence that predators are responsible for the shape of size abundance distributions is circumstantial. For instance, Hicks (1980) examined the harpacticoid copepod assemblages on marine algae at two different sites off the British coast. Eight different algae species were measured and their complexity expressed as the surface area of 1 gm of algae. One of his sample sites was clear water while the other was turbid with a high rate of sedimentation. Diversity, evenness, and species richness were all correlated with algal complexity at the clear water site but not at the turbid site. Sedimentation may have rounded out the complexity of the algae (i.e., smoothed things over), but the visual aspects of turbid water suggest fish predation had a great deal to do with the copepod assemblage.

Summary

We already knew that structure interacts with the predator and prey in a manner that helped to determine the probable survival of a given prey type. What we wanted to

find out was whether predation could structure the prey community around the physical structure of the habitat in such a manner that we can predict the shape of the animal community by examining the physical structure. The initial problem was that there is no universal way to describe a community of animals.

Numerous statistics have been published for a great variety of animal communities, each of which describes some aspect of their respective communities. The simplest of these are point sources of information describing absolute characteristics. These include abundance and richness. The statistics increase in difficulty by making them relative values. This includes statistics such as density, relative abundance, and information statistics such as diversity indices. While designed to ease comparisons between communities, they have their own shortcomings and each of them loses a great deal of information.

Researchers began to consider functions of one factor against another in an effort to retain some of the information present in the whole community. One of the simplest of these functions is rank abundance where the species are arranged in descending order of abundance and their abundance plotted as a function of their rank. Alternatively, you can plot the number of species over given abundance classes. If plotted on log-log axes, the absolute value of this slope is in fact a function representing the diversity of the community. In this way, diversity ceases to be a point value and can have different values at different points of the abundance hierarchy.

The next step was to consider abundance as a function of a more concrete factor. Normally, this other factor is size or mass of the animal. At this point, one needs to decide if you are interested in number of species versus size or number of individuals

regardless of species versus size. If number of individuals is the concern, then the comparison has to be made over a range of size classes since the probability is that no two individuals will have the exact same weight, but a given size class can have numerous individuals. Recent work suggests that all three of these factors; size, number of individuals, and number of species, are in fact related to each other and can be plotted as a three dimensional graph.

An alternative way to measure the community has been developed by Holling (c.g., Holling 1992). His method is to consider whether there are clumps or gaps in the distribution of body masses for the animals in a given community. Species are arranged in order of increasing body mass then for each species an index is calculated based on the difference in mass between the next largest and next smallest species divided by the mean mass of the species in question. Low values would indicate a clump of species with similar masses while high values would indicate a gap containing a relatively isolated species. Holling saw the distribution of clumps and gaps as reflective of the distribution of resources in the habitat and discounted predation as a causal factor.

Unquestionably, predators can impact the community. The simplest of these impacts is the elimination or reduction in number of prey species. This can occur through the killing of prey individuals or by the prey individuals leaving the area. The usual effect on the community is to reduce the overall abundance with resulting lower species richness. It is possible that a predator can increase diversity by reducing the abundance of a dominant species. If less abundant species were being out-competed, then reduction of the dominant species could allow for coexistence that would have been impossible without the predator.

Even if predators do not change the community's richness and diversity, it is still possible for them to skew the community's size distribution. Generally speaking, predators select the largest possible prey that is still convenient to handle. This results in a reduction in number of the preferred size class and apparent peaks in the abundance of prey that are either too small or too big.

Predators may also affect the community through cascades, defined as one species being affected by the predator's actions on another. Cascades can flow through the food chain and usually alternated positive and negative impacts over the trophic levels. For instance, plants may increase if a predator reduces the number of herbivores. If a secondary predator reduces the number of primary predators then the number of herbivores increase and plants decrease. If a parasite reduces the number of secondary predators, then the number of primary predators will increase, herbivores will decrease and plant species increase.

Cascades are likely more prevalent in linear food chains, but the trophic relationships of many ecosystems are so interconnected that they are better described as food webs. In those instances, adding or subtracting a species has little impact on the overall shape of the community. Among predators, there has been noted a tendency to divide the prey based on size criteria. If an additional predator is added and successfully competes for its preferred prey, then predators already in the habitat withdraw from that niche and narrow their diets. Similarly, eliminating a predator species allows other predator species to expand their diets to include those prey items being unexploited. Obviously, there are limits to the ability of a suite of predators to compensate, but if there

are a sufficient number of predator species out there, then predation can be thought of as a constant force independent of predator species acting across all scales of prey.

If predation from a suite of predators is a constant force independent of the species of the predators, then the scale of predator is unimportant. In that case, the only factors we are left with are the size of the prey items and the structure of the arena. Structure certainly impacts on the shape of the community. The simplest way is to increase the amount of structure. A bigger patch, or any area, will support a greater number of individuals with a resulting increase in richness. There is also some indication that this effect can occur in a scale specific manner. That is, changing the amount of structure of a particular size results in corresponding changes in the animal community at that size class.

Structure can also be altered by changing the variability of form in the habitat. This change in heterogeneity of form is usually measured through some sort of information index based on the Shannon-Weiner index. The relationship between heterogeneity and community richness has been well documented in terrestrial biomes but only poorly so in aquatic habitats. What is known is that the impact of heterogeneity on any given species is unpredictable, but the whole community shows a definite increase in richness in response to rising heterogeneity.

The third way that structure can be altered is to change the form of the structure. This is the factor that was developed as a concept in Chapter 3 and tested as a factor in predation in Chapter 5. While few studies have studied it explicitly, there is evidence that supports some of the basic concepts. Numerous studies have found that plants with greater surface area per unit biomass (i.e., higher complexity) support a greater

abundance of animal life, a greater density per unit area and an increased richness and diversity. This effect has also been found to occur when non-living objects form the structure. There is some indication that these statistics are a constant function of the habitat structure, forming what May (1981) called the "trophic skeleton". The impact on individual species is complex and mostly unpredictable.

The impact of a change of form on some of the comparative functions used to describe communities has also been investigated. The absolute value of the slope of rank abundance and size abundance plots seems to correlate inversely with habitat structure. In other words, simple habitats tend to be dominated by a few species. The evidence for predation as a causal factor is circumstantial, but it should be noted that peaks occur in these plots occasionally with more than one mode and that size peaks tend to be smaller in open, easily accessible areas.

It is obvious that some sort of interaction is going on. A suite of predators, influenced by structure and available prey, is influencing a community of prey items, also influenced by structure, but we do not know the nature of potential three-way interactions. Chapter 3 showed us that the structure of plants could be considered using a fractal paradigm so that complexity was strictly relative to the scale of the observer. Chapter 5 showed us that the complexity of plant material interferes with predation and needs to be examined at the scale of the animals involved. Chapter 7 will seek to investigate the interaction between whole communities and plant complexity in natural situations.

CHAPTER 7

COMMUNITY ON A COMPLEX SURFACE

We have seen that under laboratory conditions, the predator and prey interact over the surface complexity of a plant form in such a manner as to help determine the probability of a certain size class of prey item surviving a given sized predator. To what extent can this help to determine the shape of the community in a natural situation? It is tempting to extend these results and try to predict taxa' abundance patterns. However, straightforward extrapolation may prove to be misleading. Natural communities do not have just one kind of prey item. There is an entire community of potential prey taxa in competition with each other not only for resources but to avoid getting eaten. There is also a whole suite of predators not only exerting their influence on the prey but some of them being potential prey as well.

These issues must be considered along with the difficulty of manipulating an open system. The predators and prey exist in a wide range of sizes and neither can be completely excluded or isolated from other predator and prey taxa. It is possible to exclude fish, but one could not exclude predatory beetles without excluding most of the prey as well. We cannot isolate the reaction of one taxon of prey because other taxa of prey will inevitably colonize the system.

Chapter 5 showed us that statistics derived from the complexity of the plant surface could be accurate predictors of the outcome of predation events. Logically, this complexity should be represented in some aspect of the shape of the community and this chapter is an attempt to determine which aspects of community structure can be predicted

from plant complexity analysis. To accomplish this, the chapter is divided into two experiments. The first experiment is strictly observational and will be used to determine whether differences occur in the arthropod community due to the impact of plant sp. Plant material will be collected from the wild and the associated macroinvertebrate fauna tallied and measured. The resulting data will be analyzed in accordance with statistics previously developed in the literature and compared to box-counting plots of the plants. The second experiment will be similar to the first except that the emphasis will be on investigating plant form as a causative factor. Artificial plant forms will be staked out in the habitat in such a manner as to avoid the pseudo-replication of sampling monotypic plant patches. Artificial plant forms will also eliminate phytochemical influences that could potentially bias the results.

Effect of Plant species on Community Shape

Materials and Methods

The decision was made to work with *Myriophyllum spicatum*, *Vallisneria americana*, and *Hydrilla verticillata* in order to maintain continuity with the plant forms used in Chapter 5. Monotypic patches of each of the three plant species were located in Crystal River, near the city of Crystal River, Citrus County, Florida (Fig. 41). Crystal River is a spring fed, tidally influenced river along Florida's Gulf coast. All samples were taken at low tide on July 07, 1997. Water depth, at time of sampling, varied from 1.0 to 1.5 m. *Vallisneria americana* was collected at Site 1, which is into the main channel of the river and characterized by a firm sand substrate. *Myriophyllum spicatum* was collected at Site 2, which is in the mouth of a small sluggish creek, characterized by thick organic mud. *Hydrilla verticillata* was collected at Site 3, which is a partially

canalized bay, characterized by artificial stone banks. Its substrate consisted of a thin layer of mud overlying a rock and gravel substrate. All plants were rooted prior to sampling. *Myriophyllum spicatum* and *Hydrilla verticillata* plants had topped out under low tide conditions, but were fully submerged at high tide. *Vallisneria americana* plants reached halfway to the water's surface at low tide.

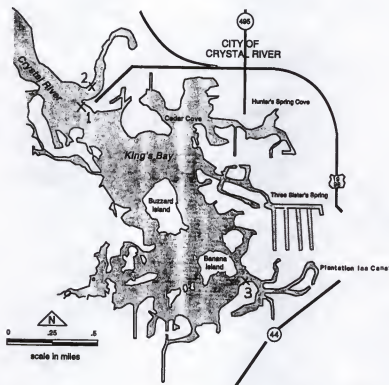


Figure 41. Map of Crystal River, Florida, showing locations of monotypic patches of aquatic vegetation. Site 1 = *Vallisneria americana*, Site 2 = *Myriophyllum spicatum*, and Site 3 = *Hydrilla verticillata*.

Individual plants were gently removed from the substrate by hand or by garden rake and floated near the water's surface. Any roots were broken off and the plants were then gently, but quickly lifted into a 14" by 24" (approximately 36 cm by 61 cm) zip lock style baggie made of 4-mil plastic. As much of the runoff water as possible was caught

in the bag. Approximately a two to one ratio of plant material to water was maintained in the samples. A bag was declared full when no more plant material could be placed into the bag without crushing. Bags were then sealed and placed on ice for transport back to Gainesville and processing. Three bags were collected from each site and an effort was made to collect each bag from a different part of the patch.

Samples were processed by gently removing plant material from the bag and allowing as much water as possible to drip back into the bag. Plants were laid on plastic grids over trays containing Professional Lysol® brand No Rinse Sanitizer as a killing agent and preservation fluid. This sanitizer is only a moderate killing agent and a mediocre preservation fluid, but it has the advantage of being directly miscible with isopropyl alcohol without producing a precipitate. The trays were placed in a humidity-reduced greenhouse and each tray was placed in a screen cage to prevent movement of invertebrates between trays. Water remaining in the bags was filtered through a fine cloth mesh to remove any invertebrates, which were then preserved in 75% isopropyl alcohol. Plant material was allowed to completely dry, given a cursory inspection, and then discarded. Sanitizer from each tray was filtered and the filtrate preserved in 75% isopropyl alcohol.

Alcohol-preserved samples were sorted under a dissecting microscope. Taxa were sight identified and the following keys used to confirm uncertain identifications; Pennak (1953) for Crustacea, Krantz (1978) for Arachnida, and Merritt and Cummins (1984) for the Insecta. Non-arthropod invertebrates were not considered for this study. Length, width, and height of each specimen were recorded and a volume of each specimen was

estimated by multiplying these three values. The mean volume of each taxon was determined as the mean of this estimate.

Results

A total of 5,296 arthropods representing 51 taxa were collected and measured. Arthropods were most abundant on *H. verticillata*, which had a total of 3,102 individuals from 42 different taxa. Next most abundant was the fauna on *M. spicatum*, which had a total of 1,388 individuals from 35 different taxa. Least abundant was the fauna on *V. americana*, which had a total of 806 individuals from 28 different taxa. Detailed results are presented in Tables 16-18.

Table 16. Number of Arachnida collected from plants from Crystal River, Florida.

		<i>Myriophyllum spicatum</i>			<i>Hydrilla verticillata</i>			<i>Vallisneria americana</i>		
		1	2	3	1	2	3	1	2	3
Actinedida	Prostigmata sp. 1				3	1	3			
	Prostigmata sp. 2	4	6	1	3	9	5	12	12	13
	Prostigmata sp. 3			1		1				
Acaridida	Astigmata			2		1	1	58	40	56
Mesostigmata	Mesostigmata sp. 1			19	5	1	3			
Oribatida	Oribatid sp 1	2	1	4	16	5	10	31	22	35
	Oribatid sp 2	3	1	10	2	8	10	3	24	25
	Oribatid sp 3					1				1
	Oribatid sp 4			12		2	2	70	16	14
TOTALS	individuals	9	8	49	29	29	34	174	114	144
	taxa	3	3	7	5	9	7	5	5	6

Using subjectively similar sample sizes could have biased abundance values. It was possible that plant sample sizes could have been different with larger samples potentially having higher abundance values. Weighing each sample to ensure their being equal, would have controlled for this bias, but would have been disruptive of the associated fauna. The sampling technique may also have introduced a taxonomic bias. Not every taxon remains associated with a plant that is being moved to the water surface.

These taxa will be underrepresented. Additionally, some arthropod taxa would not leave the plant material even if it dries completely. These taxa will also be underrepresented. These biases should remain consistent among plant species and comparisons among plant species will still be valid.

Table 17. Number of Crustacea collected from plants from Crystal River, Florida.

		<i>Myriophyllum spicatum</i>			<i>Hydrilla verticillata</i>			<i>Valisneria americana</i>		
		1	2	3	1	2	3	1	2	3
Amphipod	Amphipod sp. 1	18	19	128	448	877	472	7	5	
	Amphipod sp. 2					1				1
	Amphipod sp. 3									1
Cladocera	Cladocera	2	1	3	3	7	7	3		1
Copepod	Copepod sp. 1	56	64	61	70	151	202	1	51	27
	Copepod sp. 2	11	9	3	7	6	9			
Decapod	decapod crab								1	
	Decapod crayfish				1	3	2			
Isopod	Isopod sp. 1	1	2	18	6	9	13			
	Isopod sp. 2	4	8	1	2	2	3	18	22	7
	Isopod sp. 3							8	2	1
	Isopod sp. 4									1
Ostracod	Ostracod sp 1		3	1	5	4	4	5	10	6
	Ostracod sp 2			3	5		22			7
	Ostracod sp 3	62	82	19	58	71	63	30	24	8
	Ostracod sp 4					1				
	Ostracod sp 5		7							1
TOTALS	individuals	154	195	237	605	1132	797	72	115	61
	taxa	7	9	9	10	11	10	7	7	11

Nineteen taxa of arthropod were found on all three types of plant, including 5 taxa of arachnid, 7 taxa of crustacean, and 7 taxa of insect. Note that this does not mean they were necessarily evenly distributed among the plant species. For example, two specimens of one taxon of mite were found on each of *M. spicatum* and *H. verticillata*, but there were 154 specimens of it found on *V. americana*. Each plant species had a portion of its associated fauna that was unique unto itself. *M. spicatum* had 3 unique taxa

of insect, *V. americana* had 4 unique taxa of crustacean, and *H. verticillata* had 1 taxon of arachnid, 2 taxa of crustacean and 6 taxa of insect not found on the other two plants.

Table 18. Number of Insecta collected from plants from Crystal River, Florida.

		<i>Myriophyllum spicatum</i>			<i>Hydrilla verticillata</i>			<i>Valisneria americana</i>		
		1	2	3	1	2	3	1	2	3
Collembola	Collembola sp 1	17	7	9	9	7		22	7	13
	Collembola sp. 2	3		3		2	2		1	
Ephemeroptera	<i>Caenis nr. hilaris</i>		3	1		2	2	1		1
	<i>Callibaetis floridanus</i>					2		1		
Odonata	<i>Enallagma</i> sp.	1	1		3	5	2			
	Libellulidae					1				
Hemiptera	Gerridae			3						
	Veliidae sp. 1	77	60	56	1	6	2		1	
	Veliidae sp. 2			2						
Thysanoptera	Thrips	2		2				2		
Coleoptera	Haliplidae sp. 1				1	1	2			
	Hydrophyllidae		1	15		8	9			
Trichoptera	Hydroptilidae				3	1	1			
	Leptoceridae sp. 1				1					
Diptera	Cedidomyiidae		1							
	Ceratopogonid sp 4						1			
	<i>Bezzia</i> sp.	73	108	78	34	44	47	27	8	11
	<i>Culicoides</i> sp.			3	3	1	5			
	Ceratopogonidae sp. 3				1					
	Chironomidae sp. 1			1	48	1	41			
	Chironomidae sp. 2		16	54	52	46	37	13	9	4
	Chironomidae sp. 3	35	28	62		26	11		5	
	Chironomidae sp. 4		3	1			1			
	Ephydriidae	1		2			3			
	Stratiomyidae		3	3			1			
TOTALS	individuals	209	231	295	156	153	167	66	31	29
	taxa	8	11	16	11	15	16	6	6	4

A summarization of the richness of each class across plant species is presented in Table 19. These counts represent the combined totals for all samples from a given site. The number of taxa of Arachnida and Crustacea remains relatively constant among plant species, with arachnids ranging from 6 to 9 taxa and crustaceans ranging from 10 to 13 taxa. However, the number of insect taxa varies greatly, from a low of 9 taxa on *V.*

americana to a high of 21 taxa on *H. verticillata*. Insects represent at least half the taxa present on *M. spicatum* and *H. verticillata* but are less than one third of the taxa present on *V. americana*. While *V. americana* has fewer taxa over all, more taxa of Crustacea were found on *V. americana* than on either of the other two plant species. In general, the fauna of *V. americana* seems to be the most different of the three. In total, 8 taxa of arthropod were not found on *V. americana* that were found on both of the other two plant species. This compares to 3 taxa not found on *M. spicatum* and 2 taxa not found on *H. verticillata* that were found on each of the other two plant species.

Table 19. Distribution of arthropod taxa by class on aquatic plant samples collected from Crystal River, Florida.

	<i>Myriophyllum spicatum</i>	<i>Hydrilla verticillata</i>	<i>Vallisneria americana</i>
Arachnida	7	9	6
Crustacea	10	12	13
Insecta	18	21	9
All Taxa	35	42	28

Shannon-Weiner Diversity Indices were calculated for the total fauna on each of the plant species as well as for each arthropod class for each plant species (Table 20). Overall diversity was highest on *M. spicatum*, even though *H. verticillata* had more taxa. This reflects the fact that more than half the individual arthropods on *H. verticillata* came from a single taxon of amphipod. *Vallisneria americana* had the highest diversity of crustaceans of the three plant species but had the lowest diversities of arachnids and insects. Note that *M. spicatum* did not have the highest diversity in any of the classes, but the relatively even distribution gave *M. spicatum* the highest overall value.

Table 20. Shannon-Weiner Diversity Indices for the arthropod fauna collected on plant material from Crystal River, Florida.

	<i>Myriophyllum spicatum</i>	<i>Hydrilla verticillata</i>	<i>Vallisneria americana</i>
Arachnida	0.74	0.76	0.66
Crustacea	0.68	0.42	0.78
Insecta	0.76	0.86	0.62
All Taxa	1.09	0.88	0.77

Another way to consider evenness is to rank the taxa in order of abundance. A graph of number of individuals versus relative abundance rank would have a slope of zero if every taxon had the same number of individuals. However, the most common taxa in this study are more than three orders of magnitude more numerous than the most rare taxa, so it is difficult to interpret such a plot. It is more informative to consider a plot of log number of individuals versus log taxa rank (Figs. 42-44). In this type of plot, we consider abundance as a function of relative rank with the slope telling us the exponential scaling of abundance from one taxon to the next. The slope is of course negative, but the absolute value is inversely proportional to the evenness of the population.

From the graph we see that the most abundant taxa are relatively evenly distributed on *M. spicatum* (Fig. 42) and *V. americana* (Fig. 43), but that the arthropod population on *H. verticillata* is strongly dominated by one to three taxa (Fig. 44). The communities on all three plants are relatively even at the middle ranks indicating that most taxa fall into the middle range of abundance.

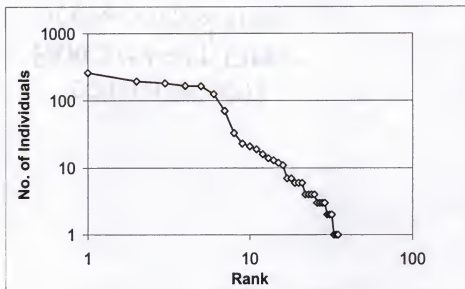


Figure 42. Rank abundance of aquatic arthropods collected on *Myriophyllum spicatum* from Crystal River, Florida.

Myriophyllum spicatum displays two tiers of abundance. There is a group of about six of the most common taxa that have roughly equal abundances. This is followed by a short but sharp decline in abundance. At about abundance rank 9, the distribution levels off to a gradual decline before dropping sharply at the lowest abundance values. *Vallisneria americana* has a sharp division between two regions. There is a disproportionate number of common taxa as well as those represented by a single individual, but there are relatively few taxa with intermediate abundance values. *Hydrilla verticillata* shows a steady decline in abundance that is difficult to divide into separate scaling regions. Possibly, there is a slight shift in scaling at abundance rank 6 and there seems to be disproportionate number of taxa represented by one individual. The relatively large number of taxa with abundance of one indicates that there is a pool of potential species out there but they do not achieve population levels.

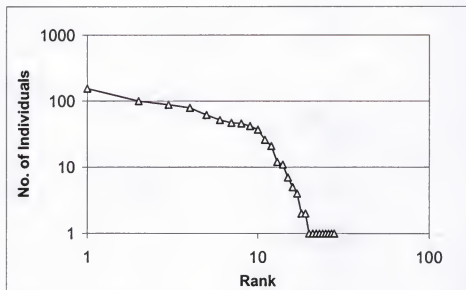


Figure 43. Rank abundance of aquatic arthropods collected on *Vallisneria americana* from Crystal River, Florida.

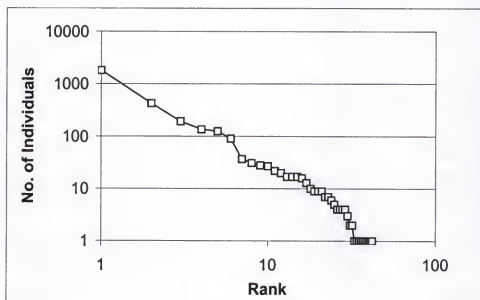


Figure 44. Rank abundance of aquatic arthropods collected on *Hydrilla verticillata* from Crystal River, Florida.

An alternative to a rank abundance graph is to segregate the taxa into abundance classes. As per the work of May (1978), abundance classes are based on $\log_2$

abundance. Thus each class n represents the number of taxa with at most 2^n individuals that did not fall into a previous class. This type of taxon:abundance plot quickly illustrates the evenness of the population. Examining the plot for *M. spicatum* (Fig. 45), we see that the distribution is bimodal. There are a large number of taxa in Abundance Class 2 to 4 as well as a smaller number of taxa centered on Abundance Class 8. The plot for *H. verticillata* is more complicated (Fig. 46). *Hydrilla verticillata* has a large number of taxa represented by a single individual (Abundance Class 0), followed by an immediate drop to two taxa represented by two individuals each (class 1). There is a steady increase in taxa per abundance class until it peaks at Abundance Class 5. There are few taxa more abundant than Class 5, but there is a hint of a mode between Class 7 and 8 and an outlying taxon at Abundance Class 10. *Vallisneria americana* has a third pattern (Fig. 47). *Vallisneria americana* has a lot of taxa represented by a single individual and a smaller number of taxa represented in Abundance Class 6 or 7 but few taxa in any other abundance level.

The follow up question to the taxon:abundance patterns is whether the observed peaks in abundance fall in and around any particular body sizes. A simple double log plot of volume versus abundance produces no apparent relationship at all (Figs. 48-50). Small and large taxa were found at all abundance levels and rare taxa come in all sizes. The scatter diagrams in Figures 48 through 50 actually show two different types of information plotted as a function of volume. The abundance of individuals is represented along the y-axis, while the number of points on the graph represents the richness.

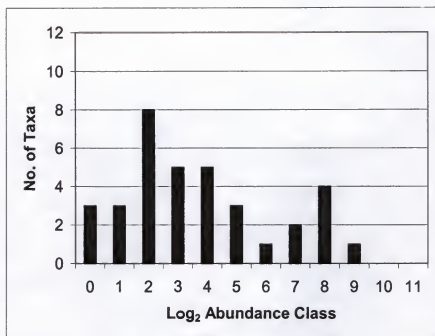


Figure 45. Numbers of taxa of aquatic arthropod in each log₂ abundance class collected on *Myriophyllum spicatum* from Crystal River, Florida.

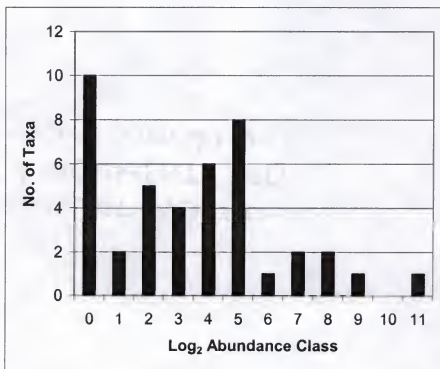


Figure 46. Numbers of taxa of aquatic arthropod in each log₂ abundance class collected on *Hydrilla verticillata* from Crystal River, Florida.

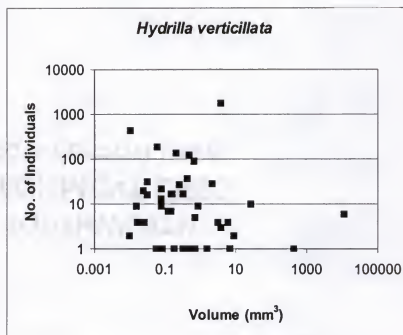


Figure 49. Abundance versus volume for aquatic arthropods collected on *Hydrilla verticillata* from Crystal River, Florida.

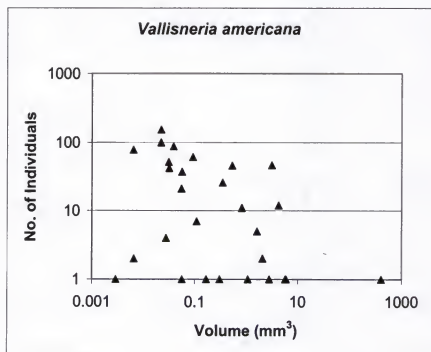


Figure 50. Abundance versus volume for aquatic arthropods collected on *Vallisneria americana* from Crystal River, Florida.

One way to examine the abundance of taxa versus size data is to plot the total number of taxa at least as big as a given volume. This is a variation on the Korcak patchiness exponent B , which was initially introduced to study the distribution of the areas of islands (in Hastings and Sugihara 1993). The exponent is derived from the following formula.

$$N(a) = \text{const} \times a^{-B}$$

where $N(a)$ is the number of islands that are at least a in size, and B is the Korcak exponent. We can determine B as the absolute value of the slope of a $\log N(a)$ versus $\log a$ graph. A low value for B over a given size range indicates that there are not many islands of that particular size. Conversely, a high value for B indicates a patch of islands of that particular size range. The technique need not be limited to islands but works perfectly well for the number of taxa of a given size. The data for this study indicates that the arthropod community of each of the plant species differs as to where the clusters and gaps are in the body size distributions (Fig. 51).

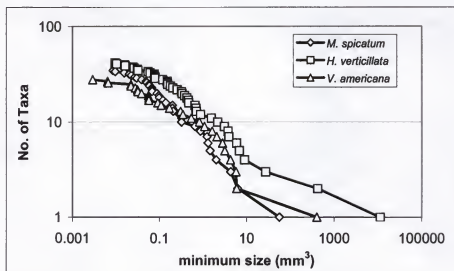


Figure 51. Cumulative number of taxa of aquatic arthropods above a minimal size on three species of plant material collected from Crystal River, Florida.

The problems with reading the information from Figure 51 are similar to those on reading the rank abundance plots. Similarly, the information becomes easier to read if we show the information as number of taxa over $\log_2$ size classes. Graphing the data in this manner, we see that *M. spicatum* (Fig. 52) has a distribution with a strong peak at body Size Class -3 and a smaller peak at body Size Class 1. The plot for *H. verticillata* (Fig. 53) has a peak at Size Class -1 and what could be described as a peak at body Size Class 2, the numbers are generally high for every size class less than 1. The plot for *V. americana* is considerably flatter (Fig. 54). Note that for *V. americana* the peaks occur at slightly larger (body Size Class 2 or 3) and considerably smaller (body Size Class -4) than for the other two plant species.

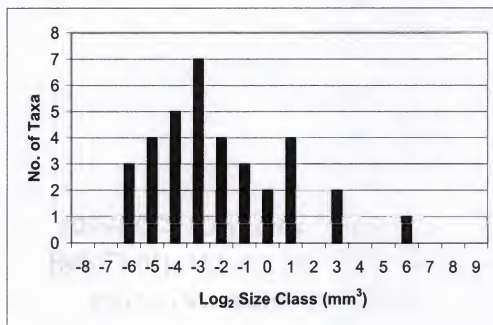


Figure 52. Numbers of taxa of aquatic arthropod in each $\log_2$ size class collected on *Myriophyllum spicatum* from Crystal River, Florida.

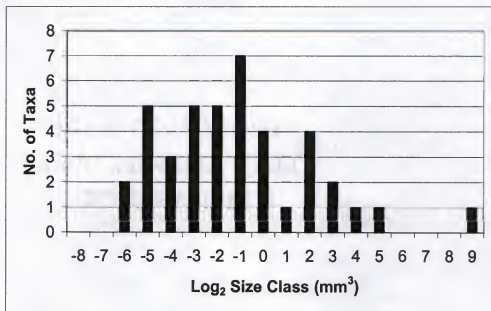


Figure 53. Numbers of taxa of aquatic arthropod in each log₂ size class collected on *Hydrilla verticillata* from Crystal River, Florida. One taxon of crayfish in Size Class 11 omitted for comparison's sake.

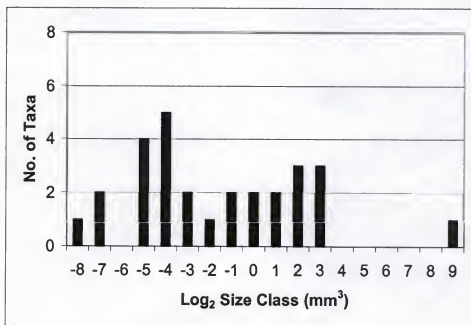


Figure 54. Numbers of taxa of aquatic arthropod in each log₂ size class collected on *Vallisneria americana* from Crystal River, Florida.

If we consider the number of individuals, regardless of taxon, per size class then there appears to be even more differences between the arthropod communities on the three plant species. Strong peaks occur roughly every second size class on *M. spicatum* (Fig. 55) resulting in six peaks, or five peaks if one lumps Size Class -4 and -3 together. The individual arthropods on *H. verticillata* fall into two strong peaks and probably three smaller peaks (Fig. 56) resulting in five peaks, or four if one lumps Size Class -2 and -1. The plot for *V. americana* can best be described as having a single peak (Fig. 57).

One problem with these types of comparisons is that they consider any two size classes to be equivalent if they have equal numbers of individuals. It is more informative to consider abundance in terms of biomass, but it becomes difficult to measure the biomass of microscopic taxa present only as a few individuals. We can get an approximation of the biomass if we assume that the body tissue of all the animals is of equal density. Volume then becomes synonymous with mass and we simply multiply the average volume of a taxon by the number of individuals present to get an estimate of the biovolume. When plotted against mean volume for each taxon we see that the results are not scattered, but appear as a loose linear relationship (Figs. 58-60). The implication of a linear relationship is biased in that it is impossible for a given taxon to have a biovolume of less than one individual, but the plots still show that there are upper limits to biomass (as estimated by volume). There is a definite trend for larger taxa to support a larger biomass, but this makes no allowances for possible competitive effects from taxa of similar size. We can look at these competitive effects by considering the distribution of biomass, as estimated by biovolume, regardless of taxon, across our now familiar $\log_2$ size classes (Figs. 61-63).



Figure 55. Numbers of individuals of aquatic arthropod in each log₂ size class collected on *Myriophyllum spicatum* from Crystal River, Florida.

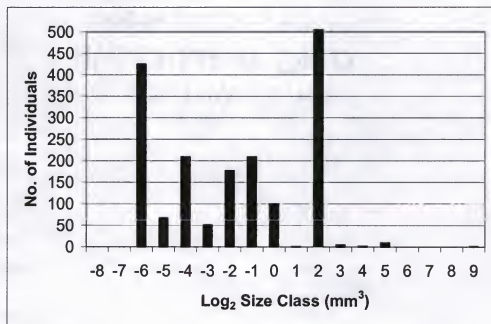


Figure 56. Numbers of individuals of aquatic arthropod in each log₂ size class collected on *Hydrilla verticillata* from Crystal River, Florida. One individual in Size Class 11 omitted for comparison's sake.

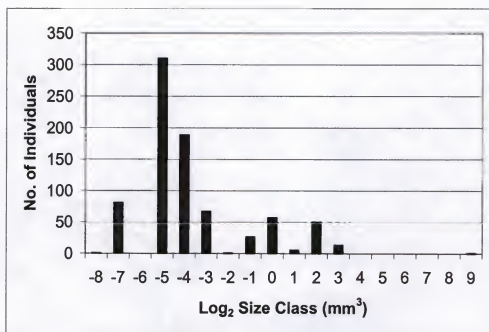


Figure 57. Numbers of individuals of aquatic arthropod in each log₂ size class collected on *Vallisneria americana* from Crystal River, Florida.

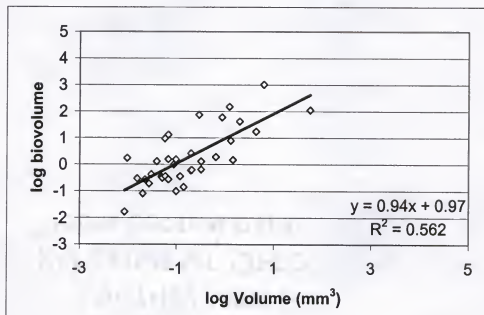


Figure 58. Biovolume of each aquatic arthropod taxon collected on *Myriophyllum spicatum* from Crystal River, Florida.

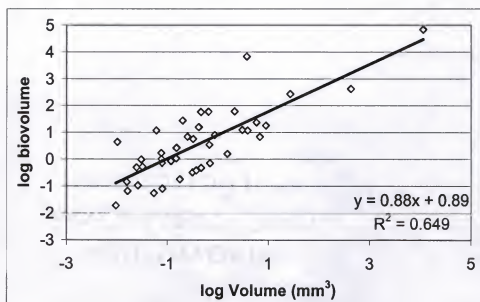


Figure 59. Biovolume of each aquatic arthropod taxon collected on *Hydrilla verticillata* from Crystal River, Florida.

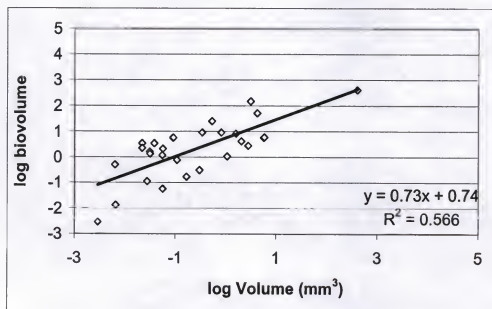


Figure 60. Biovolume of each aquatic arthropod taxon collected on *Vallisneria americana* from Crystal River, Florida.

The cumulative biomass distribution of arthropods on *M. spicatum* (Fig. 61) shows an almost log linear trend of increase up to a highest value on Size Class 3 with a second high value on Size Class 6. There are two gaps on either side of the mode and no values below Size Class -6 or above Size Class 6. The mode of the biomass distribution on *H. verticillata* is actually on Size Class 14, but there is a distinct peak at Size Class 2 with lesser, but still high values on Size Class 6 and 9 (Fig. 62). *Hydrilla verticillata* displays a more ragged appearance than *M. spicatum*. The biomass distribution for *V. americana* (Fig. 63) is much more even than the other two but is notably biased towards smaller sized animals.

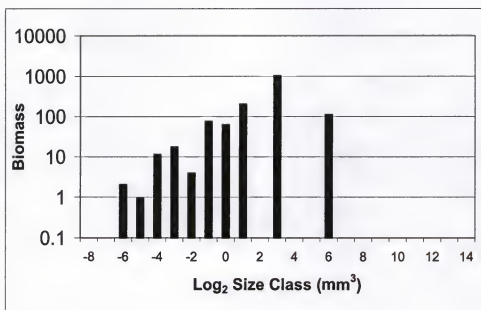


Figure 61. Biomass distribution of aquatic arthropods in each log₂ size class collected on *Myriophyllum spicatum* from Crystal River, Florida.

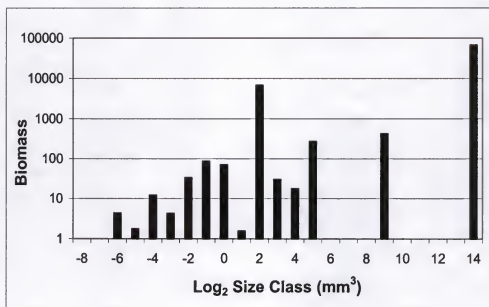


Figure 62. Biomass distribution of aquatic arthropods in each $\log_2$ size class collected on *Hydrilla verticillata* from Crystal River, Florida.

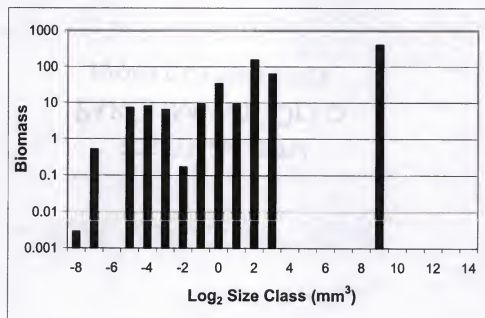


Figure 63. Biomass distribution of aquatic arthropods in each $\log_2$ size class collected on *Vallisneria americana* from Crystal River, Florida.

Techniques exist for analyzing structure in a distribution of adult animal masses. In general, the values are ranked from lowest to highest, and then a statistic is applied to the data in order to find gaps or clumps. A gap-detecting statistic developed by Holling (1992) is the Body Mass Difference Index, which in later papers is called the Size Difference Index (Holling *et al.* 1996). The index is arrived at using the following equation.

$$SDI = \left(\frac{S_{i+1} - S_{i-1}}{S_i} \right)^\gamma$$

Where S_i is the body mass of the i th taxon in ascending size rank order and γ is a de-trending exponent. Values for γ were 1.3 for boreal bird data and 1.1 for mammal data (Holling 1992). A plot of the SDI as a function of the size order results in a graph where high values represent taxa that are relatively isolated with regards to their body mass. Low values on the plot can be thought of as clumps of taxa with similar body masses. Holling (1992) arbitrarily defined a clump as at least two consecutive SDI values exceeding the mean plus 2 SE, followed by at least four values below that. Once the clumps are identified, we can determine what proportion of taxa occurs in that clump and over what size range the clumps occurs. It is then possible to compare different ecosystems by plotting these values for each clump.

The resulting plots for all three communities using Holling's body mass difference index (BMDI) are presented in Figures 64 through 66. As the BMDI values ranged over several orders of magnitude, they are presented on a log scale and no attempt was made to define a mean value for clump detection. The interpretation of these graphs is difficult, but some overall trends to appear.

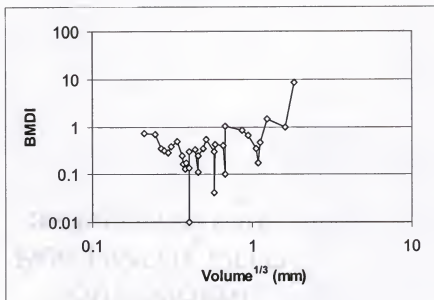


Figure 64. Body Mass Difference Index for aquatic invertebrates collected on *Myriophyllum spicatum* from Crystal River, Florida.

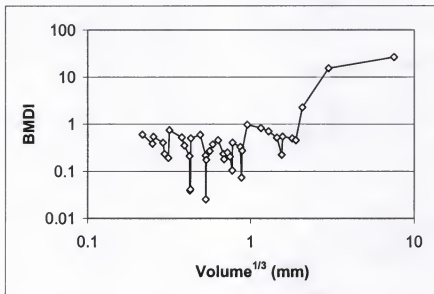


Figure 65. Body Mass Difference Index for aquatic invertebrates collected on *Hydrilla verticillata* from Crystal River, Florida.

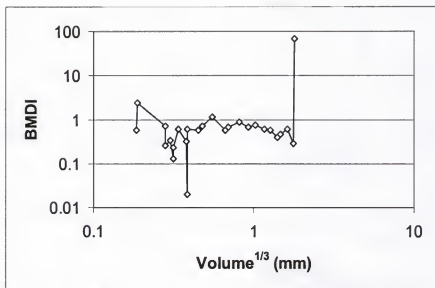


Figure 66. Body Mass Difference Index for aquatic invertebrates collected on *Vallisneria americana* from Crystal River, Florida.

The plot for *M. spicatum* (Fig. 64) seems to indicate four or five clumps spread evenly across the entire size range with few taxa lacking close neighbors. The highest gap statistic for the community on *M. spicatum* was just over 8.3. The plot for *H. verticillata* (Fig. 65) seems to indicate four clumps with a region of taxa with the larger size classes being widely spaced from each other. The highest gap statistic for the community on *H. verticillata* was just under 26.4. The plot of BMDI values for the animal community on *V. americana* (Fig. 66) seems to be very evenly distributed with one or two clumps at small sizes and one sharp "gap" at the largest size, reaching a high value of 67.4

Discussion

The animal communities were described in numerous terms. The results are difficult to grasp. The problem lies in trying to illustrate the gestalt of the animal community using two axes at a time. However, several things are apparent. The

arthropod communities can be considered as having structure in terms of size and abundance. This structure seems to correlate with the structure of the plants.

Vallisneria americana was the least complex of the three plants. *Myriophyllum spicatum* was the most complex while *H. verticillata* was of intermediate complexity. Diversity of the entire phylum as measured by the Shannon-Weiner index showed a positive relationship to this complexity gradient but the diversity of individual arthropod classes did not fit this gradient (Table 20). Insects and arachnids were most diverse on *Hydrilla* and least diverse on the *Vallisneria*. Crustaceans had the mirror pattern to this, being most diverse on *Vallisneria* and least diverse on the *Hydrilla*. Richness and abundance also followed this relationship to complexity (Tables 16-19).

Rank abundance and the related distribution of taxa per abundance class both have plant specific patterns but one that is difficult to characterize in terms of complexity (Figs. 42-47). The proportion of taxa represented by one or two individuals did increase with decreasing plant complexity (17.1% on *Myriophyllum*, 28.6% on *Hydrilla*, and 39.3% on *Vallisneria*), but in general one could not say that plant complexity led to a particular number of arthropod taxa dominating the abundance on a plant. Neither was there any clearer pattern in the distribution of number of individuals for each taxon as a function of its volume (Figs. 48-50). Paraphrasing an earlier statement, rare and common taxa occurred at all sizes.

Pattern begins to follow the complexity gradient when we consider the number of taxa, regardless of abundance, as a function of their size. Whether we look at this by considering the number of taxa at least as big as a minimum size (Fig. 51) or as the number of taxa in each size class (Figs. 52-54), we see that the arthropod taxa on the

more complex plants are more tightly clumped around the modal size class than the taxa on the simpler plants. For example, the proportion of taxa within two size classes of the modal size class is 65.7% for *Myriophyllum*, 53.4% for *Hydrilla*, and 42.9% for *Vallisneria*. Curiously, the number of individuals regardless of taxon in each size class has the opposite pattern to this (Figs. 55-57). The more complex plants have the number of individuals spread more equitably among the size classes. The arthropod community on *Myriophyllum* has six peaks in its distribution over size class, while the community on *Hydrilla* has two strong peaks and two lesser ones, and that on *Vallisneria* has one peak.

Biomass of all taxa, as estimated by biovolume, over their respective volumes has a distinct log-linear appearance (Figs. 58-60). Neither does the distribution of biomass in each size class show pattern that correlates with plant complexity (Figs. 61-63). However, the distribution of body mass clumps as measured by the body mass difference index (BMDI) does show features that seem to correlate with the complexity of the plants (Figs. 64-66). *Myriophyllum spicatum* has four or five clumps and a high BMDI gap statistic of just over 8.3. *Hydrilla verticillata* has probably five clumps and a high BMDI gap statistic of just under 26.4. *Vallisneria americana* had two clumps evident and a high BMDI gap statistic almost 67.4.

While this survey indicates that the arthropod communities on each plant species were organizationally different, it does not show that this difference was due to the structural complexity of the plants. Each type of plant material was pulled from a different site in the river. While it was not possible to collect *M. spicatum* from a *H. verticillata* patch, this does introduce the possibility that the observed structure of the arthropod communities was reacting to abiotic conditions of the site rather than to the

structural characteristics of the plants. In fact it is likely that the abiotic conditions were substantially different at each of the three sites. This was most strongly indicated by the substrate the plants were growing in. As mentioned in the Materials and Methods section, Site 1, the *V. americana* patch, had a tightly packed bed of sand. Site 2, the *M. spicatum* patch, consisted of deep layers of soft mud. Site 3, the *H. verticillata* patch, consisted of a shallow layer of mud over a basement layer of rock and gravel.

Effect of Plant Form on Community Shape

Materials and Methods

Possible confounding influence of site characteristics could only be resolved by sampling the same three plant patches again but not by sampling the plants directly. Rather, the plastic plants utilized in the fish feeding experiments were brought back into play. Six 50-g clumps of plastic plant material was prepared for each of the three plastic plant forms. One of each of the forms was tied to a tent peg with a 1 m long seine line. The peg was secured to the substrate in the plant patch with the three plant forms anchored around it in a circular fashion. Two pegs were secured at opposite ends in the plant patch at each site with the plastic plant forms spread equidistant around the peg. Each site now had two clumps of plastic plants whose form matched the plant material in that site, as well as two clumps of plastic plants whose form matched the plant material in each of the other two sites.

The plastic forms were left in the river for three months before being collected on April 02, 1998. Water depths and velocities appeared to be similar to the previous experiment, at least at time of collection. After this time, they were gently raised and slipped into separate bags for transport back to the lab. There they were vigorously

washed with a hose and scrubbed as thoroughly as possible. All overflowing water was sieved through a fine cloth mesh and the captured material stored in 70% isopropyl alcohol.

Alcohol-preserved samples were sorted under a dissecting microscope. Taxa were sight identified and the following keys used to confirm uncertain identifications; Pennak (1953) for Crustacea, Krantz (1978) for Arachnida, and Merritt and Cummins (1984) for the Insecta. Non-arthropod invertebrates were not considered for this study. Length, width, and height of each specimen were recorded and a volume of each specimen was estimated by multiplying these three values. The mean volume of each taxon was determined as the mean of this estimate.

Results

The numbers of arthropods seemed comparable to that on the natural plants. It was decided to sub-sample the material since this experiment yielded more material than the previous experiment. A four by five grid made from fine mesh was set on a pan and each sample poured evenly over all twenty squares. A twenty-sided die, commonly called a dragon die, was rolled three times. If a number was repeated, the die was rolled again until three different random numbers had been generated. All the material in the three squares corresponding to the dice rolls was collected, sorted, identified, and measured in exactly the same manner as the specimens off of the living plants. The totals reported herein thus represent 15% of the total number of arthropods collected.

A total of 4,402 arthropods were counted and measured. Richness was lower as compared to the fauna on the natural plants. There were 27 of the 51 taxa recaptured on the plastic plants as well as two new taxa for a total of 29 taxa. Detailed results for all forms at all sites are given in Table 21-23. Note that within each plant patch, abundance

was highest on the matching plastic plant form and that each plastic plant form had the highest abundance value within the matching natural patch.

Table 21. Abundance of arthropod taxa in a 15% subsample of all specimens collected on 50 g of plastic plant forms placed in patch of *Myriophyllum spicatum*, in Crystal River, Florida. (Plastic plant forms match natural vegetation as follows; M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, V = *Vallisneria americana*.)

			M		H		V	
			1	2	1	2	1	2
Arachnida	Actinedida	sp. 1		1				
		sp. 2	5		2	1		
		sp. 3	1					
	Acaridida	sp.	2		1			
	Oribatida	sp. 4						
Crustacea	Amphipod	sp. 1	35	22	31	79	20	6
		sp. 2	4	4	2	1	1	6
		sp. 4	94	27	37	41	9	4
	Cladocera	sp.					1	
	Copepod	sp. 1	2					
		sp. 2	1					
	Decapod	crab		1	2	1		1
	Isopod	sp. 1	8	8	2	2	5	2
		sp. 2	31	22	8	18	1	5
		sp. 3	55	16	8	14	9	8
		sp. 4				1		
		sp. 5	1		1			
	Ostracod	sp. 2	1	1	2			
		sp. 3	112	1	41	11	1	
		sp. 5	218		88	1		
Insecta	Collembola	globular	1					
	Ephemeroptera	<i>Caenis hilaris</i>	4	3	1	5		1
	Odonata	<i>Enalligma</i> sp.	1	1	1			
		Hydroptilidae		1			2	
	Diptera	Leptoceridae	4		1			
		<i>Bezzia</i> sp.	8		11			
		Chironomidae sp. 1						
		Chironomidae sp. 2	74	76	16	62	23	11
		Chironomidae sp. 4					1	
TOTALS	individuals	662	184	255	237	73	44	
	taxa	21	14	18	13	11	9	

Table 22. Abundance of arthropod taxa in a 15% subsample of all specimens collected on 50 g of plastic plant forms placed in patch of *Hydrilla verticillata*, in Crystal River, Florida. (Plastic plant forms match natural vegetation as follows; M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, V = *Vallisneria americana*.)

			M		H		V	
			1	2	1	2	1	2
Arachnida	Actinedida	sp. 1	5					
		sp. 2	5	3	1	5	1	
		sp. 3						
	Acaridida	sp.						
	Oribatida	sp. 4						
Crustacea	Amphipod	sp. 1	258	256	242	497	18	3
		sp. 2		1				
		sp. 4	4	3		99		4
		sp.				1		
	Cladocera	sp.				1		
	Copepod	sp. 1						
		sp. 2	4	16	10	13	1	
	Decapod	crab						
	Isopod	sp. 1	1	3		1	1	
		sp. 2			1	4	1	2
		sp. 3		2		2		
		sp. 4						
		sp. 5						
	Ostracod	sp. 2						
		sp. 3	14	12	8	7		
		sp. 5						
Insecta	Collembola	globular						
	Ephemeroptera	<i>Caenis hiliaris</i>	6			1		
	Odonata	<i>Enalligma</i> sp.	2				1	1
	Trichoptera	Hydroptilidae	5	5	4	12	2	2
		Leptoceridae				2		
	Diptera	<i>Bezzia</i> sp.						
		Chironomidae sp. 1						
		Chironomidae sp. 2	29	11	22	37	6	5
		Chironomidae sp. 4				1		
	TOTALS	individuals	333	312	288	682	31	17
		taxa	11	10	7	14	8	6

Table 23. Abundance of arthropod taxa in a 15% subsample of all specimens collected on 50 g of plastic plant forms placed in patch of *Vallisneria americana*, in Crystal River, Florida. (Plastic plant forms match natural vegetation as follows; M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, V = *Vallisneria americana*.)

			M		H		V	
			1	2	1	2	1	2
Arachnida	Actinedida	sp. 1						
		sp. 2						
		sp. 3						
	Acaridida	sp.					1	
	Oribatida	sp. 4			1			
Crustacea	Amphipod	sp. 1	11	41	145	72	5	26
		sp. 2				3		
		sp. 4						
	Cladocera	sp.						
	Copepod	sp. 1		1	8		49	
		sp. 2						3
	Decapod	crab	5	3	4	4	2	1
	Isopod	sp. 1	4	1	3			
		sp. 2	2	4	4	3		5
		sp. 3	9	18	142	29	4	8
		sp. 4	1					
		sp. 5						
	Ostracod	sp. 2						
		sp. 3	1		2		4	
		sp. 5						
Insecta	Collembola	globular						
	Ephemeroptera	<i>Caenis hilaris</i>	3	4	3	1		1
	Odonata	<i>Enallagma</i> sp.	1					
	Trichoptera	Hydroptilidae	3	2	3			
		Leptoceridae		2	1	2	13	8
	Diptera	<i>Bezzia</i> sp.						
		Chironomidae sp. 1	1					
		Chironomidae sp. 2	45	87	83	57	183	151
		Chironomidae sp. 4	1					
	TOTALS	individuals	87	163	399	171	261	203
		taxa	13	10	12	8	8	8

It is easier to compare the different treatments when the totals for individuals and taxa are presented as separate 3 by 3 matrices. Table 24 presents the total number of individuals for all arthropod taxa and shows the already noted relationship in a more

convenient format. Table 25 makes the same comparison but this time for the total number of taxa. Note that each of the three plastic plant forms has the greatest richness at the *M. spicatum* site. Also note that at each site, the plastic plant form matching *M. spicatum* either is the richest or is within one taxon of being the richest of all three forms.

Table 24. Comparative abundances of all arthropods on plastic plants placed in natural plant patches.

		River Site		
		<i>Myriophyllum spicatum</i>	<i>Hydrilla verticillata</i>	<i>Vallisneria americana</i>
Plastic Plant Form	M	846	645	250
	H	492	970	570
	V	117	48	464

Table 25. Comparative taxa richness of all arthropods on plastic plants placed in natural plant patches.

		River Site		
		<i>Myriophyllum spicatum</i>	<i>Hydrilla verticillata</i>	<i>Vallisneria americana</i>
Plastic Plant Form	M	24	13	15
	H	19	14	13
	V	13	9	11

Diversity, as measured by the Shannon-Weiner index follows a similar pattern (Table 26). The natural plant patch of *M. spicatum* has the highest diversity indices regardless of which plastic plant form is considered. The plastic plant form of *M. spicatum* has the highest index value, while *V. americana* has the lowest value in two of the three natural patches. The only anomaly is the distribution of diversity values within the *H. verticillata* natural plant patch where *M. spicatum* has the lowest index value, while *V. americana* has the highest value.

Table 26. Shannon-Weiner diversity indices for arthropod communities on plastic plants placed in natural plant patches.

		River Site		
		<i>Myriophyllum spicatum</i>	<i>Hydrilla verticillata</i>	<i>Vallisneria americana</i>
Plastic Plant Form	M	0.93	0.40	0.67
	H	0.92	0.41	0.62
	V	0.86	0.72	0.47

Rank abundance plots seem to be more similar within a vegetation patch rather than those within a given plastic plant form (Figs. 67-69). These plots mask some important differences. The most abundant taxon on one plot is most often not the most abundant taxon on another plot.

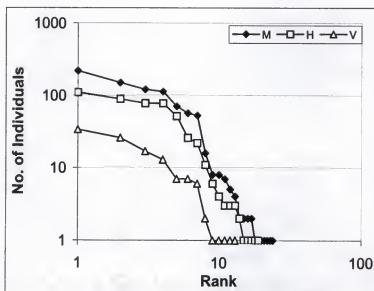


Figure 67. Numbers per taxon of arthropod expressed as a function of their rank abundance as found on plastic plant forms in a natural patch of *Myriophyllum spicatum*, Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

The most abundant arthropod on plastic *M. spicatum* within the *M. spicatum* patch (Fig. 67) is Ostracod Taxon 5. This taxon was present on only one of the two samples, so

its apparent abundance may be biased by a sampling error. The next most common taxon was Chironomidae Taxon 2, followed by Amphipod Taxon 4. On plastic *H. verticillata* in the same patch, Ostracod Taxon 4 was the second most abundant taxon, with Amphipod Taxon 1 being the most abundant, followed by a tie between Amphipod Taxon 4 and Chironomidae Taxon 2. Ostracod Taxon 4 was not even present on plastic *V. americana* in the same patch, where Chironomidae Taxon 2 was the most abundant, followed by Amphipod Taxon 1 and Isopod Taxon 3.

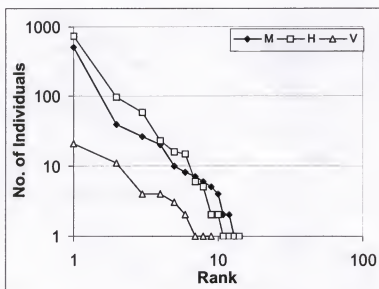


Figure 68. Numbers per taxa of arthropod expressed as a function of their rank abundance as found on plastic plant forms in a natural patch of *Hydrilla verticillata*, Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

On plastic *M. spicatum* within the *H. verticillata* patch (Fig. 68), Amphipod Taxon 1 was by far the most abundant, followed distantly by Chironomidae Taxon 2, Ostracod Taxon 3, and Copepod Taxon 2, in order. On plastic *H. verticillata* in the *H. verticillata* patch, Amphipod Taxon 1 was even more abundant, followed in second place by Amphipod Taxon 4, then Chironomidae Taxon 2 and Copepod Taxon 2. On plastic *V.*

americana within the *H. verticillata* patch, Amphipod Taxon 1 was again the most abundant, followed by Chironomidae Taxon 2, and then a series of taxa represented by only a few taxa.

Within the *V. americana* patch (Fig. 69), Chironomidae Taxon 2 was the most abundant taxon on plastic *M. spicatum* and *V. americana*, but was only the third most abundant taxon on plastic *H. verticillata*, where Amphipod Taxon 1 and Isopod Taxon 3 surpassed it.

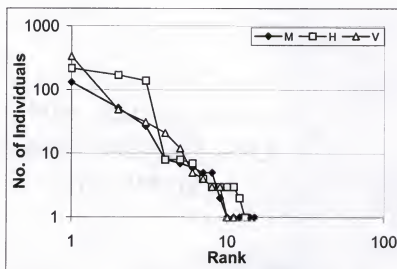


Figure 69. Numbers per taxon of arthropod expressed as a function of their rank abundance as found on plastic plant forms in a natural patch of *Vallisneria americana*, Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

The differences in the abundance of taxa on plastic plant forms within a given patch are easier to observe when looked at across abundance classes rather than rank abundance (Figs. 70-72). This is most easily noted by comparing the least abundant taxa (Abundance Class 1 or 2). Within the *M. spicatum* patch, the fauna on plastic *M. spicatum* has twice as many taxa in Abundance Class 0 and 1, as compared to the other

two forms (Fig. 70). These seem to be spread evenly among the higher taxonomic units (Table 21).

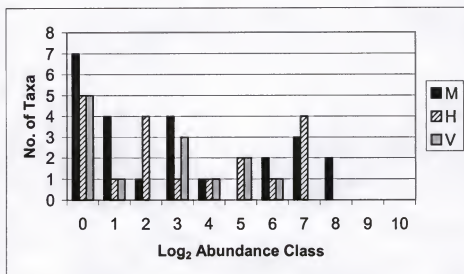


Figure 70. Numbers of taxa of aquatic arthropod in each log₂ abundance class collected on plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

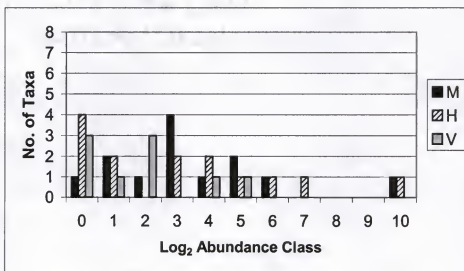


Figure 71. Numbers of taxa of aquatic arthropod in each log₂ abundance class collected on plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

Within the *H. verticillata* patch (Fig. 71), the fauna on plastic *M. spicatum* has about half as many taxa in Abundance Class 0 and 1, as compared to the other two forms (Fig. 71). Most of these rare taxa on plastic *H. verticillata* and plastic *V. americana* are present on plastic *M. spicatum*, but they manage to achieve enough numbers to be bumped into a higher abundance class. This explains the apparent peak at Abundance Class 3.

Within the *V. americana* patch (Fig. 72), the fauna on plastic *M. spicatum* has a peak of six taxa in Abundance Class 0, while the other two forms have only one or two taxa at that abundance class. While four of these six taxa (Isopod Taxon 4, *Enalligma* sp., and Chironomidae Taxa 1 and 4), were only found on the plastic *M. spicatum*, two taxa (Copepod Taxon 1, and Ostracod Taxon 3), were more common on the other two forms.

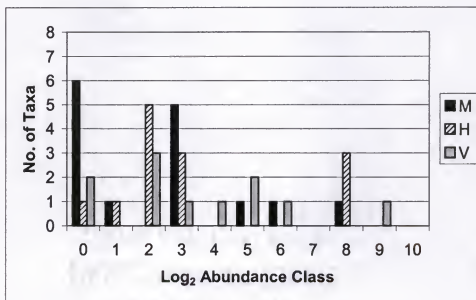


Figure 72. Numbers of taxa of aquatic arthropod in each $\log_2$ abundance class collected on plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

These trends indicate a strong impact of site on abundance distributions.

However, some differences can be associated to plastic plant form. For instance, the Ephemeroptera were always most abundant on plastic *M. spicatum*, Ostracods are never abundant on plastic *V. americana*, and Amphipod Taxon 1 was always most abundant on plastic *H. verticillata*, regardless of patch.

Plotting the number of taxa at least as big as a minimum mean size results in a pattern that is more similar within different plastic forms from the same patch than within the same plastic form from all patches (Figs. 73-75). There are exceptions though. Note that the plastic form of *V. americana* tends to have fewer taxa but always has the biggest taxon. In the natural patch of *H. verticillata*, this largest taxon was the Damselfly, *Enallagma* sp., but at the other two sites, this largest taxon was the decapod crab. Note also that the most dissimilar group of patterns occurs within the *H. verticillata* patch (Fig. 74), but the variation within the *V. americana* patch is also high at the small size scales. Interestingly, the fauna on the plastic *H. verticillata* in that patch is the first to drop out with increasing body mass. Also, *H. verticillata* lacks the smallest taxa, which are the mites and many of the smaller Ostracods and Copepods.

Looking at the plots of taxa per size class (Figs. 76-78), it becomes apparent that while there is an overall similarity within a patch, this distribution is modified by the plastic form. In the *M. spicatum* patch (Fig. 76), the fauna on plastic *M. spicatum* shows a bimodal distribution with only one taxon existing between the two peaks. This one taxon, a Trichoptera in the family Hydroptilidae, only occurred in one of the two samples, leaving the other sample with no taxa in this gap. The faunas on the other two plant forms show only a hint of this pattern, with fewer taxa in the peaks and more taxa in

the gap. The gap is filled not by the addition of new taxa, but by the change in average size of taxa (i.e., Amphipod Taxon 2 and Isopod Taxon 1 were reduced in size on plastic *V. americana*, and Isopod Taxon 2 was increased in size on plastic *H. verticillata*). In the *H. verticillata* patch (Fig. 77), all three plastic plant forms show a distinct cutoff of taxa smaller than Size Class -3 or -2. The fauna on plastic *H. verticillata* shows a similar cutoff of taxa larger than Size Class 2. The fauna on plastic *V. americana* showed nearly as distinct a cutoff, having only one specimen of the large Damselfly in one of the samples. In the *V. americana* patch (Fig. 78), the faunas on all three forms show good uniformity. is the fauna on plastic *V. americana* has the most disjunct distribution, with only three taxa (Decapod Crab, Amphipod Taxon 1, and *Caenis nr. hilaris*), being larger than 0.26 mm^3 .

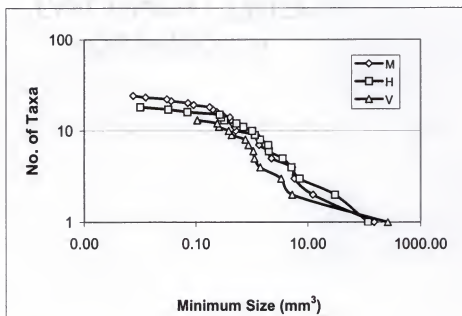


Figure 73. Cumulative number of taxa of aquatic arthropods above a minimal size on three different plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

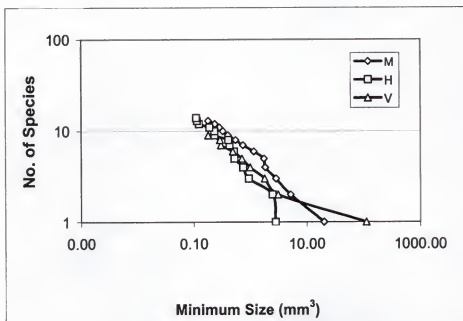


Figure 74. Cumulative number of taxa of aquatic arthropods above a minimal size on three different plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

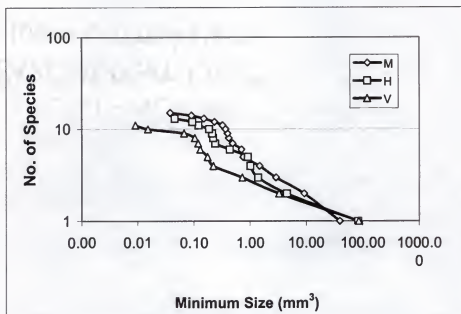


Figure 75. Cumulative number of taxa of aquatic arthropods above a minimal size on three different plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.



Figure 76. Number of taxa of aquatic arthropods in each $\log_2$ size class on three different plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

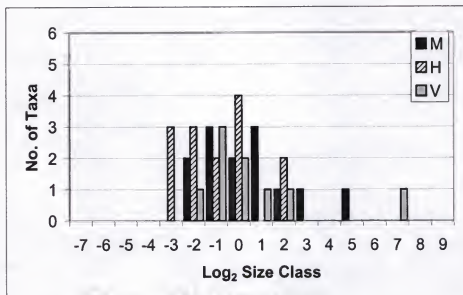


Figure 77. Number of taxa of aquatic arthropods in each $\log_2$ size class on three different plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

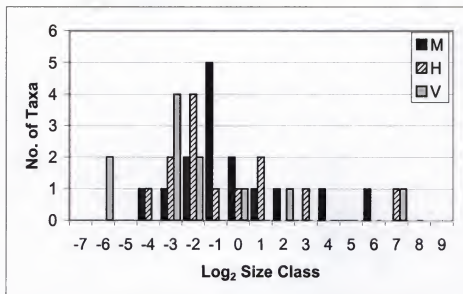


Figure 78. Number of taxa of aquatic arthropods in each log₂ size class on three different plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

A consideration of the number of individuals per size class is even more illustrative (Figs. 79-81). While the distributions are more similar within patches than among plastic plant forms, it is apparent that plastic form has a large impact on the abundance of particular size classes. The distributions within the *M. spicatum* patch (Fig. 79) show the bimodal nature of the fauna on plastic *M. spicatum* as even more apparent. The fauna on plastic *H. verticillata* shows a distinct gap at Size Class -3 and -2. The fauna on plastic *V. americana* is restricted to four size classes, between Size Class -1 and 3. Individuals in Size Class 2 dominate what appeared to be a narrow distribution of taxa in the *H. verticillata* patch (Fig. 80). Note that while plastic *V. americana* had a similar number of taxa as plastic *H. verticillata* in the *H. verticillata* patch, the number of individuals is noticeably less. The *V. americana* patch has the most dissimilar distributions of fauna on the different plastic plant forms (Fig. 81).

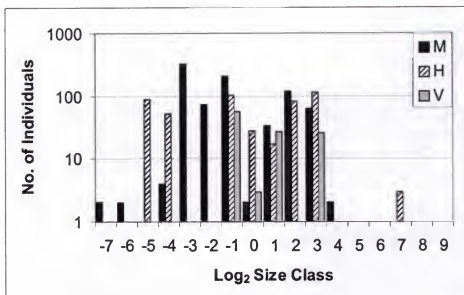


Figure 79. Number of individuals of aquatic arthropods in each $\log_2$ size class on three different plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

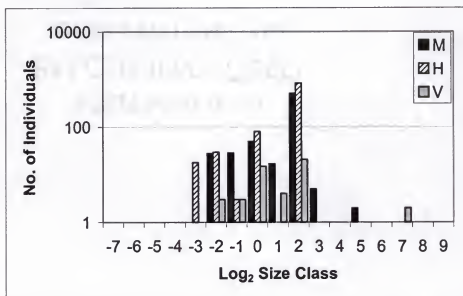


Figure 80. Number of individuals of aquatic arthropods in each $\log_2$ size class on three different plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

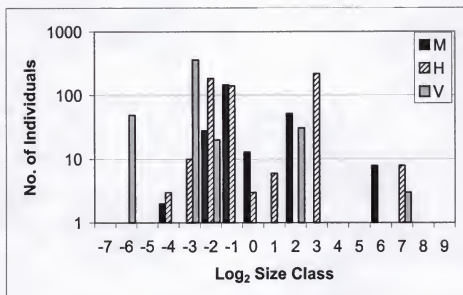


Figure 81. Number of individuals of aquatic arthropods in each log₂ size class on three different plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

As in the previous experiment, biovolume was used to estimate the biomass distribution. The distribution across size classes again reveals an overall similarity within a patch moderated by the plastic plant forms therein. The distribution of biovolume on the plastic *M. spicatum* in the natural *M. spicatum* patch (Fig. 82) shows a remarkable similarity to the distribution on natural *M. spicatum* itself as measured in the previous experiment (Fig. 61). The fauna on plastic *V. americana* also resembles this distribution but seems shifted towards larger size classes. The fauna on plastic *H. verticillata* is similar at the middle of the range of size classes, but it varies at the larger and smaller size classes.

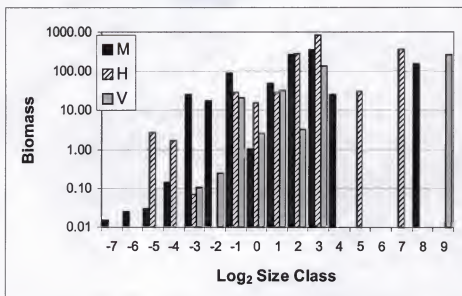


Figure 82. Biomass distribution of aquatic arthropods in each log 2 size class collected on three different plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

The distribution of fauna on the plastic plants within the natural *H. verticillata* patch appears truncated at both the larger and smaller size classes when compared to the fauna previously found on natural *H. verticillata* (Figs. 62 and 83, pgs. 234,259). The remainder of the pattern on plastic *H. verticillata* seems to be similar to the distribution on the natural *H. verticillata* (Fig. 62), even to the near absence of biomass at Size Class 1 followed immediately by the modal peak at Size Class 2. The distribution of biomass on plastic *M. spicatum* is smoother and covers more size classes than on plastic *H. verticillata*. The fauna on the plastic *V. americana* is less abundant at almost all size classes but does manage a significant peak at the largest size classes.

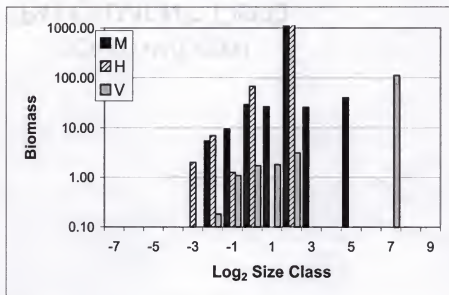


Figure 83. Biomass distribution of aquatic arthropods in each log 2 size class collected on three different plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

The distribution of biomass on plastic *V. americana* within the natural *V. americana* patch resembles the distribution on natural *V. americana* but is a little more ragged in appearance (Figs. 63 and 84, pgs. 234,260). The distributions on plastic *M. spicatum* and *H. verticillata* within this patch are also similar to that on plastic *V. americana*. The main differences being that the distribution on *M. spicatum* appears to be increasing with increasing Size Class in a log linear fashion, while that on plastic *H. verticillata* is more evenly distributed.

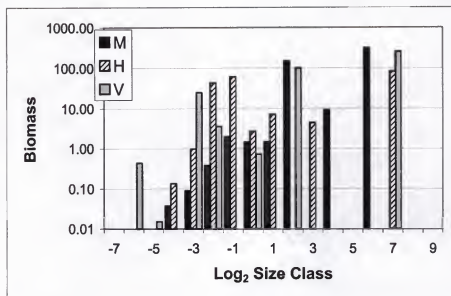
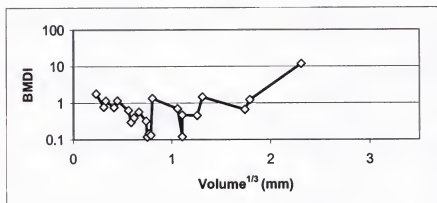


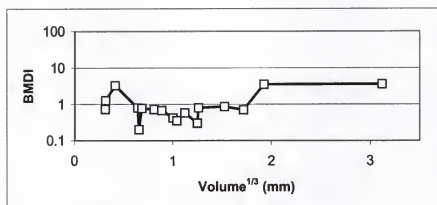
Figure 84. Biomass distribution of aquatic arthropods in each log₂ size class collected on three different plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: M = *Myriophyllum spicatum*, H = *Hydrilla verticillata*, and V = *Vallisneria americana*.

The gap analysis of these fauna, using the BMDI statistic, shows great variability, both within sites and within the same plant form (Figs. 85-87). For sake of clarity, the distributions have been drawn on separate graphs. In many ways, the BMDI plot mirrors the number of taxa over size class graphs plotted earlier, but with the relative nearness of similar sized taxa emphasized in this type of graph. The plastic *M. spicatum* fauna within the *M. spicatum* patch shows a bimodal peak as two areas of low BMDI (Fig. 84A). The fauna on the plastic *H. verticillata* seems organized into three main clumps, with a possible fourth (Fig. 84B). The fauna on plastic *V. americana* shows only one distinct clump (Fig. 84C). There is also similarity between the BMDI plot for the fauna on plastic *H. verticillata* fauna within the *H. verticillata* patch (Fig. 85B) and that on the living plant (Fig. 65). This relationship also seems to hold for *V. americana* (Figs. 66 and 86C, pgs. 237,262).

A



B



C

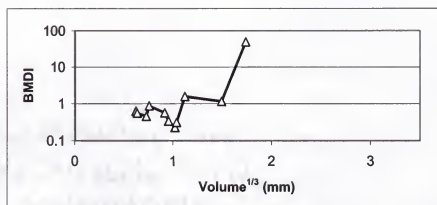
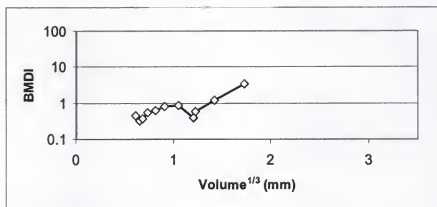
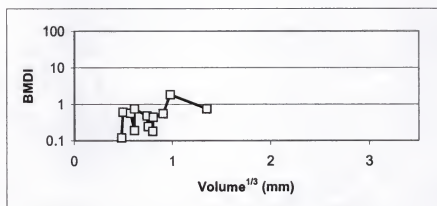


Figure 85. Body Mass Difference Index plots for fauna collected on plastic plant forms in a natural patch of *Myriophyllum spicatum* from Crystal River, Florida. Plastic forms match plants as follows: A. *Myriophyllum spicatum*, B. *Hydrilla verticillata*, and C. *Vallisneria americana*.

A



B



C

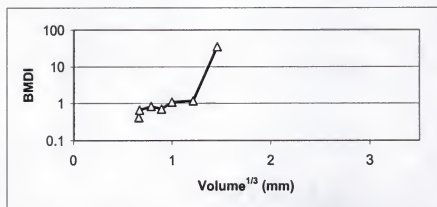
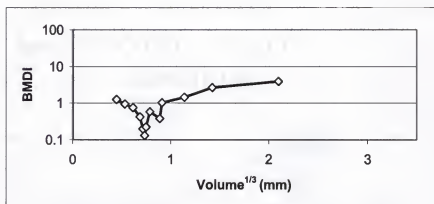
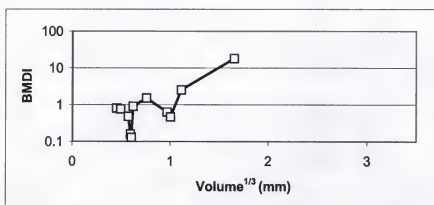


Figure 86. Body Mass Difference Index plots for fauna collected on plastic plant forms in a natural patch of *Hydrilla verticillata* from Crystal River, Florida. Plastic forms match plants as follows: A. *Myriophyllum spicatum*, B. *Hydrilla verticillata*, and C. *Vallisneria americana*.

A



B



C

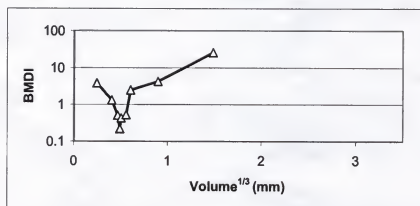


Figure 87. Body Mass Difference Index for fauna collected on plastic plant forms in a natural patch of *Vallisneria americana* from Crystal River, Florida. Plastic forms match plants as follows: A. *Myriophyllum spicatum*, B. *Hydrilla verticillata*, and C. *Vallisneria americana*.

The BMDI plots of the fauna on plastic plants from the *H. verticillata* patch (Fig. 86) show affinity to their counterparts from the *M. spicatum* patch. This is especially apparent for the fauna on plastic *M. spicatum* and on plastic *V. americana* (compare Fig. 85A with 86A, and Fig. 85C with 86C). There is a general resemblance but an overall truncation of the distribution towards intermediate sizes. Note that none of the fauna from *H. verticillata* patch extends to the smallest or largest sizes found on the fauna from the *M. spicatum* patch.

The BMDI plots of the fauna on plastic plants from the *V. americana* patch (Fig. 87) show a much greater affinity within the patch than between similar plastic forms from different patches. The plots all show a strong clump towards the small size of the range, steadily increasing to larger values at the large end of the range. A secondary clump can develop at around 1 mm, but the overall trend continues. Compare these three plots with the plots for the fauna on plastic *V. americana* from the other two patches (Figs. 85C and 86C).

Discussion

The simple conclusion would be that the differences observed in the previous experiment were due to patch differences and that observable patterns in the arthropod community depend solely on the location in the river. This is clearly not the case because placing plastic *V. americana* into either of the other two patches resulted in significant drops in abundance and richness. Even given the obvious effect on abundance and richness, there did seem to be more similarity within a patch than within a plastic plant form. However, the suggestion that location is more important than form does not consider the fact that most likely, the architecture of the sites was not significantly altered by the placement of several bundles of plastic plant. The majority of structural influence

was the natural vegetation. Rather than creating separate patches at each site and testing the reaction of the entire river fauna, all that was tested was the impact of slight structural changes to the pre-existing fauna of three different sites. Small wonder then that there was greater similarity among different plant forms within a site than within plastic plant forms among different sites.

This means that we should not expect to recreate the fauna of a *H. verticillata* patch within a *M. spicatum* patch merely by placing two clumps of plastic into it. What we can expect is the *M. spicatum* fauna modified slightly towards that of the *H. verticillata* patch. So, to analyze whether the clump of plastic *H. verticillata* affected the fauna of *M. spicatum* based solely on its shape, we should compare the fauna on the plastic plants with that of the patch it is in and with that of the patch of plant species that matches its shape.

The plastic plants have shape in common with the natural plant material. A reasonable assumption is that the fauna found on a plastic plant within a patch of natural vegetation that matches its shape represents that portion of the natural fauna responsive to shape. That being the case, then the fauna on the plastic plants that match their environment can form the baseline for our comparisons. The results for comparative abundance (Table 24) support this definition of our baseline, since the greatest abundance for all three plastic forms occurred when they matched their habitat. This means we have three baseline faunas with which to make our comparison, resulting in three axes of comparison; *M. spicatum* *H. verticillata*, *M. spicatum* *V. americana*, and *H. verticillata* *V. americana*.

If placing a mismatched plant form into a patch results in a simple blending of the biota then we would expect community indices of mismatched forms to be intermediate between those of the baseline forms. Looking at the values for richness (Table 25), we see that only four of the six mismatches fall in between their respective baselines. The ones that fail to be intermediate in value all involve placing a mismatched form into the *H. verticillata* patch. This suggests that there is something different about the fauna at the *H. verticillata* site. A quick glance at Table 22 shows that the most striking feature of the fauna at the *H. verticillata* site is that there was a huge spike in the number of larger amphipods (Amphipod Taxon 1 and 4) on the plastic *H. verticillata* and *M. spicatum* but a near total drop in abundance for all taxa on plastic *V. americana* (48 individuals for both samples total). These spikes in amphipod number account for the low diversity values at the *H. verticillata* site (Table 26). Similarly, an increase in the abundance of one taxon of chironomid resulted in a low diversity value for *V. americana* at its matching site (Table 23). Clearly, simple mixing is not what is going on.

If the resulting fauna is not simply a mixture of the two baselines, then changes must have occurred within select taxa, otherwise diversity values would not have changed. The question of whether changes occurred by changing the number of common versus rare taxa can be addressed by examining the taxa per abundance class graphs. Examining the samples from the *M. spicatum* patch (Fig. 70), we see some similarity in the distribution of taxa per abundance class. All three plastic forms support fauna that fall into roughly three abundance classes. Plastic *M. spicatum* supports peaks at Abundance Class 0 to 1, 3, and 7. Plastic *H. verticillata* supports peaks at Abundance Class 0, 2, and 7, and plastic *V. americana* supports peaks at Abundance Class 0, 3, and

5. With similar peaks in abundance and high richness of taxa, it is not surprising that there is little difference in the diversity values of any sample from the *M. spicatum* patch. The biggest difference in the three samples from the *H. verticillata* patch (Fig. 73) is that the plastic *V. americana* lacks any taxa at greater than Abundance Class 5. This alone seems to be enough to alter its diversity, but there are also differences in some of the lower abundance classes. The fauna from the *V. americana* patch was unique in that mismatching the structure in this patch increased the number of taxa (Table 25). The changes seemed to occur at the level of the rare to uncommon taxa. One way to summarize these data is to say that changing the structure in the *M. spicatum* patch resulted in slight changes across all abundance classes, changing the structure in the *H. verticillata* patch caused either little change or a dramatic drop in the most abundant animals (primarily Amphipods), while changing the structure in the *V. americana* patch resulted in sharp increases in the number of rare and uncommon taxa.

The problem with comparing abundance classes is that if one taxon is increased by the same amount another is decreased, so that they switch abundance classes, no change will be detected. Since the abundance graphs fail to consider size of the animals, this drawback becomes most noticeable when the taxa involved are of different size. The way around this is to consider the distribution of taxa across size classes.

The fauna in the *M. spicatum* patch shows the slight changes resulting from changing the structure that we observed in the abundance graphs but comparison across size class allows us to see that plastic *H. verticillata* and plastic *V. americana* are influencing different sized organisms (Fig. 76). The fauna on plastic *H. verticillata* differs from the *M. spicatum* by more than one taxon only at Size Class -2 and -1, while

the fauna on plastic *V. americana* seems to be dramatically reduced or absent at Size Class -1 and smaller. The fauna in the *H. verticillata* patch shows that both plastic *M. spicatum* and plastic *V. americana* decrease the number of small taxa and increase the number of large taxa (Fig. 77). The baseline fauna for plastic *V. americana* from the *V. americana* patch is sparse with many empty size classes (Fig. 78). Changing the structure seems to fill in the gaps and shift the size of taxa to slightly larger. The baseline *V. americana* taxa peaked at Size Class -3, while the fauna on plastic *H. verticillata* peaked at Size Class -2 and the fauna on plastic *M. spicatum* peaked at Size Class -1.

Clearly, form impacts on the community structure, but does form impact in a consistent manner? To answer this, we need to look at the graphs of number of individuals per size class (Figs. 79-81). As before, the baseline values are the distributions of fauna off of the plastic plant that matches the taxa of natural plant at each site. If we examine the baseline values and compare them to the fauna on that form at the other two sites, then we may draw insight into the nature of this impact. The baseline for *M. spicatum* indicates strong peaks at Size Class -3, -1 and at about Size Class 2 or 3. The peak at -3 is not repeated at the other two sites. The peak at -1 is not well indicated in the *H. verticillata* site and in the *V. americana* site. The peak at 2 is strongly indicated in the *H. verticillata* site and distinctly indicated in the *V. americana* site. The baseline for *H. verticillata* has one strong peak at Size Class 2 and a strong corresponding peak at Size Class 2 or 3 in both of the other patches. There is also a peak at Size Class -2, which is not present in the *M. spicatum* patch but is present in the *V. americana* patch. The baseline for *V. americana* indicates a strong peaks at Size Class -3 and smaller peaks at

-6 and 2. Size Class -3 and -6 are never indicated at the other patches but Size Class 2 does get represented.

The patterns become more obvious in the consideration of biomass distribution (Figs. 82-84). Within the *M. spicatum* patch (Fig. 82), plastic *H. verticillata* leads to less biomass in Size Class -2 and -3, which represents the lower cutoff of its own baseline. It also leads to a reduction in the size of the largest taxon, the crab, which never attains that size in its own baseline. Still within the *M. spicatum* patch, plastic *V. americana* causes a general reduction in biomass over all size classes except the largest size class (Size Class 9, the crab taxon). *V. americana* has this exact same impact on the biomass in the *H. verticillata* patch (Fig. 83). The baseline biomass distribution of *H. verticillata* has a narrow range with three sharp peaks and two intervening valleys. The baselines of both *M. spicatum* and *V. americana* lack these valleys and so these forms tend to fill in these gaps, as well as extending the distribution of biomass into larger size classes. A similar phenomenon occurs within the *V. americana* site (Fig. 84). The baseline distribution of *V. americana* has numerous gaps, which are partially filled in the distributions on the other two forms in the *V. americana* patch. However, neither of the other two forms was able to support biomass at the smallest scales that *V. americana* was able to, with small specimens of Chironomidae Taxon 2.

So we see that form does impact on the size and abundance of the fauna, but does this change the ability of taxa to coexist? The BMDI plots seem to indicate there is some truth to this. Recall that the BMDI plot of the fauna from a given plastic form in the *M. spicatum* patch resembled the plot of the fauna from the matching form in the *H. verticillata* patch. There also seemed to be an overriding similarity between all plots

either on plastic *V. americana* or from one of the other forms within the *V. americana* patch. The indication is that plant form plays a strong role in the distribution of taxa body masses.

Conclusions

We introduced this Chapter by arguing that the predator prey interaction across a complex form, such as a plant, should impact on the distribution of arthropods on that plant. Clearly, plant form impacts on the arthropod community and at least within the context of a preexisting fauna, shape of the substrate can determine the size and frequency of the fauna on it. This is a long way from proving that predation has shaped these communities around the form of the plant. However, much of the data in this chapter could be considered as consistent with that of predation being at least a major force in the shaping of the arthropod community. To clarify this statement, reconsider the work done in earlier chapters.

Recall from the box-counting experiments that each of the plants sampled in this section was distinctly different in the distribution of complexity across scale. While three plants were linear at the smallest scales, *Vallisneria americana* was the most linear and remained fairly linear up to the point where the scale began to exceed the mean width of a blade. This is what would be expected from a grass-like plant with wide flat blades. *Myriophyllum spicatum* was the most complex of the three and stayed complex almost to the smallest through largest scales measured. Again, this is what would be expected from a multi-branched plant consisting of whorls of finely divided leaflets. *Hydrilla verticillata* was intermediary between the other two plants. At larger scales, *H. verticillata* appeared complex reflecting that it also is composed of tight whorls of

leaflets. At smaller scales, *H. verticillata* becomes linear at a much lower resolution than *M. spicatum*, reflecting the fact that *H. verticillata* leaflets are larger and more complete in appearance than *M. spicatum* leaflets.

Recall from the fish predation experiments that a given prey's vulnerability to a given predator was found to be consistent with a function of its accessibility and detectability. The models used to estimate these factors were derived from the relative sizes of predator and prey and the apparent difference in available space as perceived by the two. On a low complexity surface, one can change the sizes of predator and prey a great deal before there is any real difference in prey vulnerability. A high complexity surface on the other hand, a slight increase in the size difference between predator and prey results in a significant decrease in the prey's vulnerability. Furthermore, this decrease in vulnerability becomes greater as the surface complexity increases.

Nominally, this sounds like the overriding selective force on prey items is towards smaller sizes. While this would work against a single type of predator, animals in the wild are subjected to an entire suite of predators occupying almost all size scales. Becoming too small for one predator would just drop you in the jaws of the next smaller predator. Alternatively, one could outgrow all of one's predators, but this would not work if there were always bigger predators to take up the slack. Assuming that the predation pressure is constant across size class, then the expected distribution of prey should be a smooth distribution where the number of prey individuals parallels the complexity of the surface.

However, none of the plant surfaces examined here have a perfectly constant complexity. Each of them is linear at small scales and develops increased complexity

only at scales near the size of major features of their construction. Reading roughly off of the box-counting plots, this occurs at about 0.3 mm for *M. spicatum*, 2.0 mm for *H. verticillata*, and 6.0 mm for *V. americana*. These values correspond roughly to half the size of their respective leaflets. In addition, *H. verticillata* shows a zone of reduced complexity occurring at roughly 15.0 mm corresponding to the size of its whorls.

An alternate survival strategy can work on a surface with at least two zones of varying complexity. If an animal of a given size is in one zone of complexity and the next larger zone is less complex, then growing bigger helps survival by outgrowing a small number of potential predators but at the risk of a large drop in the potential cover from larger predators. If, on the other hand, the next bigger zone is more complex, then growing larger allows an animal to outgrow some of its predators with negligible drop in protection from larger predators. This should especially hold true when moving from a linear zone to a complex zone.

This suggests that predation pressure would be lowest at the scale resulting in an increase in complexity and it should be highest in a zone of decreased complexity. Linearity always increases predation pressure. This pressure is worse with increasing range of linearity since this results in a loss of cover from larger and larger predators. Lower predation should allow for the survivability of more individuals and this does seem to be upheld by the individuals per size class graphs. The fauna on *M. spicatum* show a distinct peak in individuals at Size Class -3 (Fig. 79), which corresponds to a volume of 0.0625 to 0.125 mm^3 , or its linear equivalent of 0.40 to 0.50 mm length. *M. spicatum* was able to support a relatively significant number of arthropods at the scales at all three sites. The fauna on *H. verticillata* show a distinct peak in individuals at Size

Class 2 (Fig. 80), which corresponds to a volume of 2.0 to 4 mm³, or its linear equivalent of 1.26 to 1.59 mm length. This peak was strongly presented at all three sites. The fauna on *V. americana* had no peaks larger than Size Class -3. The long range of linearity may have prevented significant populations from building up at scales larger than the thickness of a leaf, or those animals were somehow excluded from collection. However, *V. americana* did manage to maintain a few individuals in every patch at the scales corresponding to the width of a blade (Size Classes 7 to 9). *H. verticillata* was also able to maintain a few individuals at these scales which would correspond to the size of their whorls. While the number of individuals at these large scales is small, the biomass distribution graphs indicate that a substantial biomass, as estimated by biovolume, is maintained at these levels (Figs. 82-84).

The number of individuals or total biomass as a response to predation pressure is relatively straightforward. It is much more difficult to predict the numbers of taxa sustainable under a given level of predation. At risk of oversimplification, predation can both increase and decrease the number of taxa in an area. If predation is absent, then competition controls the number of taxa present and the population tends to be dominated by the best competitors. Relatively low levels of predators tend to select the most abundant prey and allow less common animals to gain against the superior competitors and richness goes up. High levels of predation eliminate competition as a controlling factor and only the few taxa capable of surviving the predatory onslaught are left.

Assuming the above scenario is accurate and that predation does structure the community, then high number of taxa would indicate moderate predation levels, low number of taxa with high number of individuals would indicate low predation levels, and

low number of taxa with low number of individuals would indicate high predation levels. If the shift in zones of complexity is a driving factor in predation risk we should be able to predict where there would be peaks in the number of taxa. For *M. spicatum*, maximum refuge should be attained at Size Class -3. Lowest predation implies dominance by one or two taxa, which is what is found on *M. spicatum* at Size Class -3, and other scales (Fig. 76). The number of taxa per size class increases with increasing scale while still maintaining fairly high population levels, which would be as predicted from increasing predation rates. Decreasing scale leads to the linear zone resulting in high predation and low population levels. For *H. verticillata*, maximum refuge should be attained at Size Class 2, but only Amphipod Taxon 1 and 4 occupy that size class with more taxa occurring at lower size classes (Fig. 77). There are no taxa or individuals at greater than this scale, implying intense predation or a complete absence of food resources. This latter is a potential given the abundance of amphipods at this scale. At scales smaller than Class 2, there is a sharp drop followed by higher numbers of taxa, implying an intense predation rate followed by moderate predation levels. For *V. americana* (Fig. 78), there is a low number of taxa at almost all scales except for a peak of two taxa of Crustacea, a Copepod and an Ostracod, and two taxa of Insecta, a Leptoceridae and a Chironomidae, occurring where the number of individuals spiked (Size Class -3). The interpretation here is that *V. americana* offers little refuge at any scale except for slight relief at a small scale, perhaps representative of the thickness of the leaves. This interpretation helps explain why adding mismatched plant forms increased the number of taxa present, namely adding structure provided refuge.

None of these interpretations are proven. A great number of other possibilities exist, e.g., reproduction and immigration, to name two. The interpretations presented here should be considered as working hypotheses that help explain some of the nuances of community structure but they require further study. So far this chapter has just begun to explain the size-abundance relationships between animals and habitat, but this is a good point to stop and reconsider all that has been learned with respect to the entire work presented here. The following chapter is intended to review all preceding chapters, discuss them in context of each other, present final conclusions, and make suggestions for future research.

CHAPTER 8

SUMMARY AND CONCLUSIONS

The purpose of this project had been to determine whether the structural aspects of the area of introduction determine the successful introduction of a species into an existing community. Specifically, it was thought that the shape of plants offers a refuge from predators, but that the refuge was not a constant. Instead, the level of refuge was hypothesized to be dependent not only on characteristics of the plants but also on the size and frequency of predators and prey.

The attempt to model this relationship had to proceed in a three-step process. First, an objective method of quantifying the shape of objects had to be established. Secondly, it had to be shown that the shape of the plant influenced the interaction between predator and prey in a quantifiable manner. Thirdly, it had to be shown that actual populations responded to this shape in such a manner as to control the abundance of particular species.

The order of these steps was arrived at in a backward manner. It was noted that in a biological control program, insects released against a target weed did not always establish. Since the insects had plenty of food and they initially came from an area of similar climate, it was usually suggested that predators eliminated the insects. In other cases it was noted that some insects would occur in dramatically differing numbers on different species of plants even though laboratory testing suggested there should be no preference. Again, predation is often suggested as a causal factor.

The implication is that plants vary in their ability to provide cover. If it were possible to characterize the shape of the plant, then one may be able to predetermine the possible abundance of a given species. Before we can determine the impact of cover on a whole community, we needed to determine the way shape interacts between predator and prey. And before we could investigate the impact of shape on the interaction between predator and prey, we needed a numerical way of comparing plant shapes in an objective manner.

Measurement of Form

A problem arose in that quantitative descriptions of plant form had not been adequately developed. Fractal geometry had been proposed as such a descriptive technique but much confusion exists as to the exact method of analysis. The mathematics is quite clear when one is considering the inherent dimension (i.e., the dimension of the process to create the object). This is nothing more than the Hausdorff-Besicovitch dimension, which is derived from the ratio of the number of replications of the object to the apparent size of the object. This is virtually impossible to determine for an irregular shaped, preexisting object.

Box counting dimension had been developed as a technique for estimating the Hausdorff-Besicovitch dimension but has been poorly understood and frequently misapplied. The main problem is that the Hausdorff-Besicovitch dimension is estimated at scales approaching infinitely small size. Natural objects do not have one scaling region but can have many different complexities over numerous different scaling regions. In order to overcome this, the concept of apparent dimension was developed. Apparent dimension is a measure of how complex an object appears to be at a particular scale. It

can be directly measured by the box counting technique if one works under the constraints of three axioms.

Axiom 1 is that no object can be measured as being smaller than the scale of measurement. The most important point of this axiom is that any object can be considered a point if it is measured at a large enough scale. Previous box counting techniques considered only the slope as scale approached infinitely small size. This axiom frees us to consider what happens when scale is increased.

Axiom 2 states that complexity is strictly relative to the scale of measurement. This frees us from the idea that objects have a fixed dimension that describes their physical existence. Rather than being the slope of the limit as scale approaches infinitely small sizes, complexity should be thought of as a multi-scale function. This means that an object can simultaneously have numerous dimensions nested within its structure and while it may appear fractal to one observer it can appear linear to another.

Axiom 3 lies at the heart of perception or indeed of any interaction with a surface. It states that the probable outcome of an interaction is determined as a continuous averaging function across scale. This introduces the concepts of probability and averaging into consideration. Probability acknowledges that odd and unlikely events can and do occur. This means that it is impossible to exactly predict one single instance of interaction. Averaging allows us to predict what the probable outcome will be as long as we average across all scales at which the interactions are occurring. More importantly for this work is that axiom 3 removes the necessity of finding the minimum box count at each scale. The average count is taken to be the most probable level of interaction and therefore the value needed to determine a probable outcome.

These three axioms allow us to consider the box counting plots generated for the images of the twelve aquatic plant species. The images were all linear at the smallest scales, but axiom 1 allows us to consider structure at larger scales. They all have variation in their complexities (Fig. 14) and one could be tempted to use maximum dimension as a measure of complexity. However, axiom 2 tells us that all scales are equally valid and axiom 3 says that interaction is not at one particular scale but averaged across scale. This means that the mean human response to an image's complexity can be accurately predicted by the average complexity across all scales. That is, it would be accurately predicted if box-counting is a legitimate measure of the object and not some artifact. The high R^2 value (0.96) for the regression of human response against computer generated mean dimensions indicates that the Richardson effect is real and not a trick of measurement. Furthermore, box-counting measures this phenomenon in a way that corresponds to human perception.

This is not the first study to compare human perception with fractal dimensions. Pentland (1986) generated planar patterns and asked people to estimate their "roughness". Cutting and Garvin (1987) generated polygonal shapes and asked people to rate their complexity. Both studies found strong correlations between human perception and the dimension of the generated images. These works differ from the current work in that they were dealing with generated objects with known inherent dimension. The objects were not measured *a posteriori* and then correlated with perception. While they certainly lead the way by showing that perception can be quantified through fractal geometry, they did not show how this could be applied to the perception of natural objects.

Perception is a complicated issue. Attempts to make objective measurements of this subjective phenomenon led to the science of psychophysics. While not restricted to vision, this is the type of perception we are most concerned with here. Humans are visual animals and many predators hunt visually. Vision is concerned with the nature of surfaces, as is fractal geometry. In addition, there is a great body of literature on the different philosophies of visual perception. Most of these can be divided into two schools of thought (Bruce *et al.* 1997). Traditional theories emphasize the inferential and constructive nature of perception. They argue that inference is required to build up an image from the flat static field. In other words, bits and pieces of the image field are associated and put together in order to perceive objects.

The ecological school of thought is somewhat different. Based on the work and theories of J.J. Gibson from the 1950's through the 1970's, it is based on a continuum through time and a direct perception of the environment. Both of these are somewhat similar to axiom 3. The input is taken to be the image structure in the optic array, so that the entire image is taken in at once, not unlike the cross scale features discussed above. However, no image is perceived until movement occurs. This too is reminiscent of dynamic averaging leading to a probability event. It is beyond the scope of the current paper to settle the differences between these schools of thought, but it is interesting that the current work does tend to support the ecological school of thought.

Certainly, the first part of this report did establish that it is now possible to quantify the human perception of complexity. The question naturally arises as to how well this can be extrapolated to a non-human observer. Clearly there are some similarities between human and animal perception. The now classic observance of

industrial melanism in the peppered moth (Kettlewell 1973) suggests that the predatory birds are observing the light and dark moths in a manner similar to humans. However, there is also good evidence of distinct differences between human and animal perception. Dittrich *et al.* (1993) trained pigeons to react to pictures of wasps. They then presented these pigeons with pictures of hover flies, thought to be Batesian mimics. The birds did respond to the hover flies but ranked them in terms of their similarity to the wasps in an order that was different from that of the human observers.

The point of the first part of my study was not to come up with a universal model of perception. Perception was the tool used to analyze form. A method was needed to measure form in a manner that was objective, numerical, repeatable, and real in a biological sense. From this perspective, it does not matter that fish perception is probably different from human perception. The salient feature is that this perception experiment was used to calibrate box-counting as a valid tool in the analysis of shape. Clearly the computer analyzes the images in an objective manner, it puts out numerical charts and graphs that are repeatable for any image, and the numbers correspond to the real biological action of the mean human response. The use of box-counting is clearly a valid technique to quantify form in biological experiments.

Form as an Interactive Surface

Having established the non-linear nature of surfaces and being able to quantify the complexity of the surface, it became possible to consider the act of predation as an interaction between the three variables: size of predator, size of prey, and complexity of habitat. This interaction was tested by setting up artificial arenas consisting of 1-gallon glass bell jars partially filled with 3 liters of clean well water. The model predator was

chosen to be the eastern mosquitofish (*Gambusia holbrooki*) and the model prey was 3rd instar larvae of the yellow fever mosquito (*Aedes aegypti*). Complexity of habitat was changed by adding plastic plant material that was a close match to one of three species of aquatic plant: *Myriophyllum spicatum*, *Hydrilla verticillata*, and *Vallisneria spiralis*.

The relationship between size of predator and size of prey is reasonably simple. Increasing the size of predator resulted in more prey being consumed. From this obvious relationship, we derived the formula that determined the expected number of third instar mosquito larvae that would be consumed by a mosquitofish of a given size over a 24-hour period. This was taken to be the base predation rate for this system. In no way is this to be construed as some universal constant. The relationship in this particular system was needed to determine what if any effect adding structure would have. Any potential impact could therefore be interpreted as to how it compared to the base predation rate.

It had been deduced that the effect of structure would most likely occur through the actions of detectability and accessibility. Detectability was defined as a function of the size of the prey divided by the size of the habitat and that it was independent of predator size. Accessibility, on the other hand, was a function of the size of the arena as perceived by the predator divided by the size of the arena as perceived by the prey. It was thought that both functions would come into play and help predict the number of larvae eaten. The first experiment did not support this. Accessibility multiplied by base predation rate did have a lot of predictive value ($R^2 = 0.731$), but detectability multiplied by base predation rate had little ($R^2 = 0.145$). The implication of these results is that detection was not a problem but that the accessibility of prey to the predators was important.

It was thought that this experiment might have inadvertently been biased against finding detectability as significant. This was because detectability, as defined, is independent of predator size. This experiment hinged on altering predator size, and so while some detectability changed when the plant forms were changed, it might not have been enough to be detected with this experiment. The experiment was repeated except that predator size was kept constant and prey size was varied. Accessibility multiplied by base predation rate was still predictive ($R^2 = 0.776$) as a logarithmic function, but detectability was even less predictive ($R^2 = 0.019$). It appeared that detectability was not a factor, but by varying larval size, it was possible to consider how detectability affected predation success within the context of just one plant type. If only results from a single plant form are considered, then the accessibility function multiplied by the base predation rate becomes a linear model with higher predictive values ($R^2 = 0.754$ for no plant cover, 0.826 for *V. americana*, 0.824 for *H. verticillata*, and 0.796 for *M. spicatum*). Even more interesting, the detectability multiplied by base predation becomes highly predictive ($R^2 = 0.839$ for *V. americana*, 0.830 for *H. verticillata*, and 0.830 for *M. spicatum*).

Both accessibility and detectability are important in determining the vulnerability of a potential prey item. The relationship between these two is unclear. Why should accessibility be universally applicable across plant forms while detectability seems to be determinable within a plant form? Both are derived from simple measurements of form and so should logically transmit across forms, but they do not. If we assume that there is no dramatic change in the search behavior of the predator on different forms (none was apparent), then the answer probably lies in the third dimension.

Recall that our box-counting plots were based on flat scans of pressed and dried plant specimens. All details of special structure in the third dimension were lost and therefore not incorporated into any of the calculations. If the added degree of difficulty of a third dimension was roughly equivalent between the plants, then calculations of risk based on form can be accurately determined from the box-counting plots. If on the other hand the degree of difficulty from an added dimension is not the same between plant forms, then the box-counting plots will only allow accurate predictions within a plant form. This latter seems to be the case for the detectability function. The accessibility function was at least able to be determined as having a logarithmic relationship between the plants.

If we assume that the third dimension is approximately as complicated as the other two, then the affect should be noticed in the linear slopes of actual kill versus (accessibility $\times$ base predation rate) graphs. We can use the results of accessibility $\times$ base predation rate as a mini test of this hypothesis. In other words, being slightly complex in two dimensions implies only slight complexity in the third dimension and only a slight increase in this slope. On the other hand, being highly complex in two dimensions implies high complexity in the third dimension and a larger increase in this slope. The slope of these graphs should therefore be in order of the plant's complexity and this does seem to be what is occurring (Table 11). Box-counting based on two-dimensional scans can only be thought of as an estimate of the full range of structural complexity. Unfortunately, this researcher does not have access to the high-level imaging and computer programming needed to make three-dimensional cube-counting plots.

The whole concept of the impact of the arena on predation is intimately linked to the concept of refuge. Exactly what constitutes a refuge in a predator-prey system is not clearly understood. At its most basic, a refuge is taken to mean a physical area where in the prey is safe from attack by the predator. However, a refuge has also been taken to mean anything that provides protection from predation including; invulnerable age or size classes, development of a temporary physical protection, flight, timing of activity, or continuous dispersal (Glass 1971; Heck and Orth 1980; Woodin 1981; Peterson 1982; Stoner 1982; Crowder and Cooper 1982; Coull and Wells 1983; and McNair 1986). Refuge can also be considered as a protection from any potential mortality source, such as physical disturbance (Woodin 1978). McNair (1986) considered only physical areas providing temporary protection to be refuges and specifically excluded other definitions. Although far too exclusive, McNair's definition comes closest to defining the complexity of the environment (fractal or otherwise) as forming the refuge of interest.

The early workers on refuges in predator-prey systems constructed miniature arenas where the effects of a refuge could be observed directly and then described mathematically. Gause (1934) set up a test-tube arena with unicellular predator (*Didinium nasutum*) and prey (*Paramecium caudatum* Ehrbg.). If no refuge was given, the predator would always consume all the prey then starve to death. If a refuge of "oaten medium" was given, then the outcome was no longer certain but instead three different outcomes could occur with varying probability. It was possible that the prey would all be consumed anyway and the predators starve. It was also possible that enough prey would be in refuge that the predator would starve and only prey were left. Finally it was possible that predator and prey could co-exist with enough prey leaving refuge to

support the predators and enough prey remaining in refuge to reproduce. In other words, adding a refuge helped to stabilize the predator-prey oscillations allowing co-existence.

Huffaker (1958) found a similar response by increasing the relative refuge present. Working with one species of mite as a predator and another as prey, he measured the population fluctuations as they were allowed to roam over an arena of oranges. He found that if the oranges were simply placed close to each other with little obstacles to travel between them, the predator and prey would oscillate with increasing amplitude resulting in extinction of one or both. If however, the environment was made more complex by introducing barriers between the oranges, then some areas could temporarily act as refuges allowing for more stable oscillations and at least temporary co-existence of predator and prey.

Currently, most of the work on refuges is being done in the computer using mathematical models. The modeling of a refuge has followed the lines of modifying existing population models such as the Lotka-Volterra or the Nicholson-Bailey. Although refugia vary in the amount of protection they provide, the usual method of incorporating them is to consider that either a constant number of the prey is safe in the refuge or that a constant percentage of the prey is safe (Maynard Smith 1974; Murdoch and Oaten 1975). Maynard Smith (1974) found that a constant proportion of prey in a refuge had no effect on the stability of the Lotka-Volterra model, which exists as a neutrally stable cycle. A similar result was found for the Nicholson-Bailey model where the dynamics remain a series of oscillations of increasing magnitude (Allen and Gonzalez 1975).

The results were somewhat different if a constant number of prey items were assumed to be in the refuge. In this case, the Lotka-Volterra model's equilibrium changed to that of an asymptotically stable point (Murdoch and Oaten 1975). The presence of a constant number of prey items in a refuge had an even more dramatic impact on the dynamics of the Nicholson-Bailey model (Allen and Gonzalez 1975). As the number of prey in a refuge is increased, the increasing oscillations that are typical of the model decrease. Eventually the predator and prey cycle in a stable limit cycle. Increasing the number of prey in refuge even further results in both predator and prey achieving non-trivial equilibrium points.

Overwhelmingly, the mathematical evidence suggested that a refuge was a stabilizing force. McNair (1986) had some difficulties with some of the assumptions of the modeling. Essentially he thought them too simplistic and cited Gause (1934) as finding that a refuge can stabilize a population and allow co-existence but does not guarantee it. His main addition to the assumptions was that he allowed refuge-seeking prey to be encountered by the predator and that there was a probability that the prey did not find the sanctuary of the refuge. In other words, he envisioned the prey making a dash for refuge when the predator showed up. Interestingly he found that adding a refuge was capable of destabilizing equilibrium. Furthermore he found that the destabilizing effect could occur if either a constant number or a constant proportion were in refuge. Essentially he found that the stability condition for the positive equilibrium point is that the predator functional response must increase faster than the total prey birth rate. If this was the case before a refuge was added, then adding a refuge allowed the birth rate of the

prey to increase while suppressing the predator functional response. The result is that life would become harder for the predator.

The importance of the functional response in the stability of the relationship could prove to be of importance. Allen and Gonzalez (1974) found that functional response increased linearly with temperature, something that was assumed within the construct of the model. This suggests that changes in temperature can change the stability of the model resulting in the same amount of refuge having different effects at different temperatures. This has been found to be the case at least mathematically. Collings (1995) found that for at least one model there is a temperature range in which increasing the amount of refuge destabilized the model.

Mathematical evidence suggests that the amount of refuge is important in deciding which animals can co-exist within a given habitat, but how does structure create refuge? The behavior of the prey item can combine with structure to create a relative refuge. This is the case with caridean shrimp in seagrass beds (Main 1987). Whenever a pinfish was present, the shrimp would move around to the other side of a grass blade. They kept their eyestalks showing so they could watch the predator and stay on the opposite side of the blade. More often, we think of refuge as physical structures within which a prey item could hide. Walter and O'Dowd (1992) examined the distribution of phytoseiid mites on leaves and compared them to the distribution of domatia. Domatia are mite-sized structures in the vein axils of leaves from woody angiosperms. These were found to shelter predatory mites so that leaves with domatia had much higher numbers of phytoseiid mites than those without. This was found to hold true between plants of the same species, between two different congeneric species, and between

unrelated species. Experimental blockage of the domatia resulted in numbers of phytoseiid mites dropping to 24% of the control. Structure as refugia from predation has been modeled and validated for at least a few other systems (Levin 1973; Smith 1972; Luckinbill 1973; and Smith and Tyler 1972, 1975).

The measure of accessibility devised in this work can be thought of as the inverse of refuge. For example, let us consider a situation where a prey item hides in holes and that the size distribution of the holes is fractal. In this case the number of holes an animal could fit into would be a constant multiplied by the size of the animal raised to the power of $3-D_f$, where D_f is the dimension of the distribution. Note that the smaller the animal, the more holes it can fit into. Now assume its predator is larger than the prey. This predator-prey relationship would have a given level of accessibility. The number of holes the predator could fit into would be fewer with the difference in number of holes representing a constant refuge dependent on the size of both animals.

There is some evidence that a disproportionate number of small insects are found within a refuge. California red scale is a pest of citrus that has been demonstrated to be more common underneath the bark of the trees it is infesting. There was some evidence that the interior was in fact a refuge since removal of ants, which were thought to help create the refuge by attacking parasitoids, caused the scale populations to fluctuate in a less stable manner (Murdoch *et al.* 1995). Earlier instars are of course smaller and were found in disproportionate number within the refuge (Walde *et al.* 1989; Murdoch *et al.* 1989).

Pontasch (1988) implied that complexity is intimately linked with refuge. He created artificial streams and measured the predation rate of a predatory stonefly

(Plecoptera) feeding on mayfly naiads (Ephemeroptera). Three different types of substrate were considered. The simple substrate consisted of a layer of fine sand. The complex substrate had a layer of pebbles overlaying the layer of sand. The intermediate substrate had the sand and pebbles mixed together. Predation rates were highest on the simple substrate and lowest on the complex substrate. Predation rates were intermediate on the mixed substrate. The different rates were attributed to there being more refugia in the more complex surfaces.

Early works led to the entrenchment of the idea that a refuge was a stabilizing force and helped to preserve a prey species from extinction. There are a few instances where this has been found to be true in natural systems. Snails heavily prey upon a barnacle, which is under such intense predation that it cannot co-exist with the snail. It survives only because it can successfully live in areas less frequently inundated by tides where the snail can not survive (Connell 1970). These areas provide the refuge that allows for coexistence. Another example of refuge allowing coexistence is that of several species of corixid, which could only survive in the same pond as trout if there was dense vegetation present to act as a refuge (Macan 1976). In a rather circular argument, Hawkins *et al.* (1993) conducted a general literature study on any parasitization rates of insects. They reasoned that all hosts not parasitized were in refuge and that therefore the literature supports the idea that a greater amount of refuge leads to a stronger tendency to persist when under attack. The problem with this interpretation is that it defines refuge as not being attacked and then states that refuge prevents attack. Chance could produce the same conclusion, if one uses this definition.

However, refuge clearly is important in determining predation levels. The literature suggests that refuge can have some influence on what species can coexist. Given that the models of accessibility and detectability seemed validated, how would this be extended to the community level? Using box-counting to measure form allowed us to predict the predation rates for a given predator and a given prey combination. The third part of this study attempted to extend the scale of this predictability to include wild populations.

Form as a Community Template

The third and final part of this study was concerned with evaluating whether predation is influenced by plant complexity such that the shape of the arthropod community is altered. As discussed in the previous section, complexity has been strongly associated with our understanding of refugia and refuge availability has been shown to allow coexistence of species that would normally exclude each other. One example comes from northern Wisconsin, where the introduced crayfish *Orconectes rusticus* (Girard), is replacing *O. propinquus* (Girard), which had previously invaded and begun replacing the native species *O. virilis* (Hagen). Largemouth bass prefer smaller crayfish, *O. propinquus* is smallest and so loses to *O. rusticus*. The native species, *O. virilis*, is biggest but loses in competition for refuge to the other two species. Thus, when faced with a predator, *O. virilis* loses to competitors and when faced with a competitor, *O. virilis* loses to predators (Garvey *et al.* 1994).

Cooper and Crowder (1979) formalized the idea that structural complexity would shelter "vulnerable" species. They speculated that these species would be found more often in areas of increasing structural complexity. One of the few manipulative studies of

the interaction of predators and cover value on an open community of prey items was Leber (1985). Predatory shrimp were caged out on seagrass beds so that prey items were free to come and go. Complexity in the cages was changes by clipping the sea grass or adding red algae clumps. The effects of changing complexity were species specific. Some species were negatively impacted by the predators at one complexity level but not at the other. Other species were never impacted.

Another study showed that the type of refuge was unimportant as long as refuge was provided. Caley and St. John (1996) created artificial reefs using stacked pipes, open on both sides. Complexity was added by screening off one or both ends of the pipes. Screening off one side only leading to "transient refuge", or both sides leading to "permanent refuge". No proof was offered that predation caused the observed community changes, but no significant difference could be measured between transient and permanent refugia. This suggested that the two types of refugia were equivalent.

These studies concentrated on particular species while in this study, the community was examined as an abstract whole. There was a fairly good relationship between the complexity of the plant form and the species richness of its associated fauna but not the overall abundance of individuals. A major exception was that the fauna from the live *H. verticillata* was the richest measured (42 species). This may have been a sampling artifact since there is a well-known relationship between sample size and number of species represented. The plastic form samples were of a more uniform sample size (each was 50-g mass) and clearly showed this relationship, at least between the forms that matched their sites. These results seem to agree with Lawton (1983) who found that the richness of the arthropod fauna on plants did follow a complexity gradient,

at least for terrestrial plants. To paraphrase, one can say that richness follows the gradient trees > shrubs > perennial herbs > annual weeds. Lawton did not rule out, or control for, the age of the plants studied, and so this evidence could be confounded with time.

It was a curious point of the current study that abundance of individuals did not seem to follow complexity of plant material. This may have been impacted by physical differences of the sites involved, since a given site only contained one species of plant. Krecker (1939) was one of the first to quantify the fauna on submerged vegetation. While he did not measure plant complexity, he did measure the number of individuals per unit length of plant material. He found that for every 10 feet of plant material strung together, *M. spicatum* had 1,442, *Elodea canadensis* (a close morphological match to *H. verticillata*) had 564, and *Vallisneria spiralis* had 30 individuals. Unfortunately, he made little allowance for the branching of the plant material. Indeed, Vincent *et al.* (1991) found that neither *M. spicatum* nor *V. americana* correlated with species richness or overall abundance of gastropod species in the St. Lawrence River. Only 3 of the 7 most abundant species showed significant covariance with plant species. Overall, the effect of plant species was weak compared to site and year. The authors suggested that the gastropods were calcium limited.

Diversity was another statistic that did not correlate well with plant complexity. While the most complex plant, *M. spicatum* had the highest diversity levels, there was little difference between *H. verticillata* and *V. americana*, whether one considered real plants or plastic forms. Overall, other than species richness, single number statistics of

community structure were poor correlates of plant complexity. Again, this might have been biased by the inability to collect each plant species at every site.

Relative abundance functions did not fair much better. There was a strong indication of species-specific pattern but not one that tied well with plant complexity. The rank abundance graphs (Figs. 42-44 and 67-69) showed a strong similarity between the fauna collected on a plastic plant from a matching patch and the natural plant within that patch. *M. spicatum* had a group of several species dominating the abundance, *H. verticillata* had one or two, while *V. americana* showed no overwhelmingly abundant species. The relationship was not strong.

Historically, the explanations for population dominance by a species have been ascribed to resource availability models. MacArthur's (1972) broken stick model involved imagining the environment as a linear gradient, or as a "stick". This stick is simultaneously broken into a number of pieces equal to the number of species occupying the environment. If the amount of resources available to a species, represented by the size of the piece of stick, were proportional to its abundance, then the distribution of rank abundance of all species would be lognormal.

A lognormal abundance curve would resemble a straight line if drawn on a log-log plot. Of all the abundance curves in this study, the fauna on *H. verticillata* comes closest to being a straight line. Neither of the other two appears straight. Seemingly, this would indicate that the abundance curves are not the result of resource availability. The graphs illustrating the number of species in each abundance class (Figs. 45-47 and 70-72) do not clarify this situation. They do show strong similarity between the fauna on the

natural plants and the fauna on the plastic plants in their matching sites. This helps to validate the use of the plastic plants in the second community sampling experiment.

Graphs where species are plotted according to their size as well as their abundance are termed abundance space according to Lawton (1990) and there are numerous ways to represent this data. One of the simplest is to consider each species as a point on an X-Y scatter diagram of number of individuals versus body size.

Unfortunately, our data do present much information in such a plot (Figs. 48-50). Lawton (1990) maintained that the species near the upper bound of this space would be near to being resource limited and therefore should scale as their body mass^{-0.75} since that is the general form of the relationship between body mass (W) and metabolic rate (Peters 1983). This has been found to be the case for some studies (Damuth 1981; Peters 1983; Peters and Raelson 1984; Peters and Wassenberg 1983; and Brown and Maurer 1986) but not for others (Morse *et al.* 1988). One would be hard pressed to find such a relationship in the data found in this study. Lawton's diagram suggests that there is a lower bound, representing the minimum frequencies for a given body mass. Whether this is in fact the case remains yet to be proven. Much of the difficulty in determining this lies in the problem of adequately sampling small, rare species. No such lower limit was found in our data.

Lawton (1990) divided the constraints on the coexistence of species of similar mass into horizontal partitioning rules, i.e., competition, and vertical partitioning rules, i.e., trophic relations. Lawton considered horizontal partitioning rules as the determining factors controlling whether species of a given mass may occupy a local area when another species is already present. In essence, competition between two or more species

may be severe enough that they are mutually exclusive on the local scale even though they may coexist as part of the same regional fauna. He does acknowledge the competition for predator-free space (*i.e.*, predation) could be considered as one of these horizontal factors.

To date, there is as yet no clear consensus on whether differences in the observed body masses of coexisting species are due to competitive pressures or simply the result of random sampling from a limited pool of potential species. Juliano and Lawton (1990a,b) performed a study that helped to shed light on this problem. They studied the coexistence of dytiscid water beetles in northern England. Not only did they examine the natural populations, but they also created random assemblages of beetle species drawn from the regional list of species present and they created assemblages of "pseudo-species" by drawing random points from within the full range of available morphological space. Large, well-buffered water bodies that contained predatory fish had beetle assemblage that were more regularly and widely spaced than would be expected by chance. Beetle assemblages from small, acid pools that lacked fish were not significantly different from random assemblages. These results seem to indicate that the beetles were not resource limited and thus did not exclude each other based on competition for resources. However, under the influence of predatory fish, which supposedly resulted in competition for predator-free space, some beetle species were mutually exclusive. The authors caution that merely because competition for resources did not occur within this system, it might be a structuring feature in other communities.

A fundamental feature determining how many species can occupy a given size class depends on the number of individuals in that size class. In fact, Siemann *et al.*

(1996) found a simple relationship between the number of species and the number of individuals. For sweep samples of grassland arthropods, the number of species in a given ($\log_2$) size class was about equal to the square root of the number of individuals in that size class. This relationship seemed to hold across a 100,000-fold range in insect body sizes (Siemann *et al.* 1996), but it does not seem to hold up well to the data in this study.

May (1978) and Morse *et al.* (1988) determined that all relationships of abundance per species, number of species, and body size class were all related. Morse *et al.* (1988) determined that a three-dimensional plot of log abundance per species versus number of species versus log body size class revealed a relatively simple surface at least for the beetle community of Bornean tree canopies. In contrast, Basset and Kitching (1991) performed much the same sort of study on Australian rainforest tree species. Their three-dimensional plot was similar to the Bornean beetle data but much rougher with sharp differences between size abundance classes. The Australian study involved daily sampling over two years, which the authors thought could emphasize and alter the number of species per log abundance classes. A sub-sample of the first four weeks of the study produced a noticeably smoother curve.

There has been a lot of work and speculation as to what should control the number of species within a size class. Much of it is based on the metabolic arguments summed up neatly in Peters (1983). Explanations about a species' abundance based on comparisons of energetic demands assume that the animals being compared have equal access to fixed levels of food resources. The abundance of a given species relative to another is a function of how efficiently each species metabolizes that energy and how much energy each species needs for maintenance. This statement should be made clearer

with the following example. Hemmingsen (1960, *in* Peters 1983) found that the standard metabolic rate of homeotherms ($R_{s(h)}$, in Watts) was dependent on the body mass of the species (W , in kg) according to the following power law:

$$R_{s(h)} = 4.1 W^{0.751}$$

Similarly, the standard metabolic rates of poikilotherms ($R_{s(p)}$) has been found to be determinable from the following power law (Peters 1983):

$$R_{s(p)} = 0.14 W^{0.751}$$

Note that if a poikilotherm and homeotherm have equal body mass, then the standard metabolic rate will be higher in the homeotherm. This means that a given level of food resources can support a greater number of poikilotherms than homeotherms of the same body mass.

The data in this study do not support a power law relationship between size and abundance. What seems to present itself is a pattern where each plant form has a certain number of peaks that tend to occur at certain size classes. This seems to be loosely tied to plant complexity since *M. spicatum* had more peaks than *H. verticillata*, which in turn had more peaks than *V. americana* (Figs. 55-57).

Certainly, simple log-series do occur in nature. Mittelbach (1981b) found that if the number of invertebrates in a Michigan lake were plotted as a function of their size class, the distribution fits a lognormal curve. His data showed an interesting relationship between substrate types once it was graphed in a form similar to that in this study (Fig. 40). His data also showed a steady decline in size as season progressed. It is unknown if this was caused by predation but size decline was certainly reflected in fish gut contents. Seasonality was not considered for this study, and represents a potential weakness. The

current results represent a snapshot in time, with no guarantees that the relationships continue over time.

Maurer and Brown (1988) examined all species of terrestrial birds in North America north of Mexico. They divided 380 species into arbitrarily defined logarithmic mass classes. Within each size class, population energy usages (thus relative abundances) fit a log-series. The most abundant species in each size band uses the same fraction (~10%) of the total energy used by that size band. The small size classes were more densely packed with species. This implies that the parameters that determine how resources are divided up are not identical for all body sizes even though the qualitative rules within a size class appear to be the same.

Maurer and Brown (1988) also looked at the distribution of biomass with respect to body size for the North American avifauna. Some previous studies suggested that biomass would be distributed evenly across the body mass octave. The North American birds do not show this type of distribution. Rather, biomass was found to increase with increasing body mass octave even though the density of species was decreasing. This relationship was also reflected in the arthropod fauna collected in this study (Figs. 61-63 and 82-84). However, the data in this study do not show a smoothly increasing relationship. Rather, there are peaks and valleys, the pattern of which seems to be plant form specific.

The equal energy use hypothesis (Van Valen 1973; Damuth 1981) states that the energy used by a population of a large species is equal to that used by a population of a small species. This hypothesis gave poor estimates of the energy used by North American birds. The energy used by small species was overestimated and the energy

used by large species was underestimated. The species density compensation hypothesis (Harvey and Lawton 1986) suggests that the energy used by small species will be greater than that used by large species. Even though a given small species might use less energy than a large one, there are more species of small organisms. The North American bird data did not support this hypothesis either. Rather than steadily decreasing as theory predicts, the energy usage actually increases, then levels off with increasing body mass.

Holling (1992) also realized that the distribution of body masses of animals was not smooth in its distribution. Certain scaling regions would occur that appeared to have an unusual high or low number of species at that range of body sizes. The distribution appeared to be clumped. It was an attempt to draw a relationship between this clumping and the shape of the environment that led to the creation of the Body Mass Difference Index (BMDI). It was thought that this index was representative of the fauna's use of the environment (Holling *et al.* 1996). It was reasoned that resources would be distributed in the environment in such a manner as to be most efficiently utilized by species of particular body sizes. This would lead to a one to one relationship between structural features of the environment and clumps within the BMDI plot.

The arthropods, collected in this study, also show a clumped distribution of body masses and their BMDI plots do show trends that tend to follow form-specific patterns (Figs. 64-66 and 85-87). It is hard to envision the observed patterns as being reflective of the distribution of resources, though. While one may argue that leaves, stems, other plant parts, and the periphyton thereon may vary in inherent quality, the distribution of gaps and clumps do not match the scales representing the size of these structures. Indeed, the size classes with the greatest number of individuals show up as neutral values on the

BMDI plots. This is not to say that the BMDI clumps cannot be reflective of the distribution of resources at greater scales. After all, most of these animals are quite capable of traveling fair distances. However, this study cannot justify a resource distribution explanation for the shape of the BMDI plots.

The preponderance of the evidence seems to suggest that resource or energy distributions were not responsible for the majority of the patterns observed in this study. Form as a determining factor of community shape is indicated, perhaps most strongly by the distribution of arthropods on plastic plant forms. Consistencies within one plastic plant form did occur, among different plant patches. The fauna on *H. verticillata* was always more abundant than that on *V. americana*. The same was usually true for the fauna on *M. spicatum*. Unsurprisingly, species richness tended to follow the abundance values. *M. spicatum* always had the richest fauna or was within one species of being the richest, while *V. americana* always had the least number of species.

In spite of some consistencies among plastic plant forms, there was an overall similarity in the distributions on all forms placed in a particular patch. This is just an extension of the concepts of island biogeography developed by MacArthur and Wilson (1967). These ideas can be simplified by saying that the local fauna must be a subset of the regional "source" fauna. This phenomenon has been shown numerous times. By way of example, Ambrose and Anderson (1990) found that artificial reefs had a localized influence on the fauna of the surrounding soft-bottomed sediment. Baelde (1990) found that the fish community of seagrass meadows was strongly influenced by nearby environments. Different fish communities were found in two meadows even though the same species of seagrass dominated both meadows. Smaller day-active fish dominated a

meadow near the mangrove estuaries. It functioned as a fish nursery and its populations pulsed with the reproductive cycles of the mangrove fish. Slightly larger night-foraging fish dominated a meadow located nearer to a coral reef. Population fluctuations at this second site were smoother. It was thought that the coral reefs supported more piscivorous fishes, which made it dangerous to remain in the meadow during daylight. Applying these results to the present study, it seems unreasonable to assume that one type of form will have the same pattern of arthropods at every site. The impact of form should be looked for in how a mismatched form impacts on the fauna already there. Nonetheless, this suggests a weakness in the current study from selecting single sites of each of the three plant species.

Placing a mismatched form into a patch did reduce richness present in natural *M. spicatum* and *H. verticillata* but actually increased the richness in the natural *V. americana* patch. In all three patches, most of the changes occurred with the number of rare species. Consideration of the number of species over size classes was even more indicative. Placing plastic *M. spicatum* into a mismatched patch always shifted the peaks of the preexisting fauna towards larger size classes. Plastic *H. verticillata* had a similar effect on the fauna in the natural *V. americana* patch, but when placed in the natural *M. spicatum* patch, its main effect was to reduce the smaller size range peak of the bimodal distribution. Placing plastic *V. americana* into a mismatched patch created a larger size class, but reduced the size range of the remaining species.

Equally interesting was the pattern created by mismatched forms in the distribution of number of individuals over size class. Placing plastic *M. spicatum* into a mismatched patch shifted the peak of individuals towards smaller size classes in the *H.*

verticillata patch but towards larger size classes in the *V. americana* patch. Plastic *H. verticillata* had a complementary effect by shifting the peak of individuals towards larger size classes in the *M. spicatum* patch and towards much larger size classes in the *V. americana* patch. Plastic *V. americana* had the effect of reducing overall numbers at all size classes. This effect was strongest in the *H. verticillata* patch.

Whether predation caused these effects is unknown, but this is certainly possible. Some evidence indicates that increasing the variability of the predator allows for greater variation in prey distribution. Butler (1989) found that cages with varying numbers of bluegill led to increases in the size and size range of some invertebrates, most notably in the Odonata. Varying predator density also resulted in prey items becoming more heterogeneous between patches and an increase in temporal variation. Increasing predator variation had no effect on total prey abundance, species abundance, or within-patch spatial heterogeneity.

The best evidence of predation as a causal factor is that in the graphs of individuals per size class, there was a strong tendency for the number of individuals to peak at particular size classes that conformed to structural characteristics of the plant forms. While not proving the correlation between structure and abundance as being caused by predation, it could happen that structure allows a prey species to find its predator-free space. The reasoning is that animals can outgrow some of their predators. Thus, for the most part predation risk comes from larger predators. As found in Chapter 5, larger predators are slowed from base line feeding when structure acts to reduce detectability and accessibility of prey. Detectability and accessibility are determined by the complexity of the plant surface and are directly measurable off of a box-counting

plot. Solid structural characteristics of plants tend to have box-counting plots with slopes near 0 (i.e., linear). Increasing the size of a prey animal on a complex surface outgrows a percentage of the predators but at the expense of increasing detectability and accessibility to the remaining predators. In contrast, on a linear surface, increasing the size of a prey animal still outgrows a percentage of the predators but has minimal impact on detectability and accessibility to the remaining predators. Selection would tend to favor animals that were at the size of major structural characteristics of the plant resulting in the observed abundance peaks.

Prey species would find their predator-free space in the shadow of the structural features of the plant. Some corroborating evidence for such a "predator shadow" comes from mismatched forms creating abundance peaks in patches where they did not occur. While the forms could not be expected to create peaks of size classes that did not occur at those sites, there were some notable peaks. Although it is difficult to line peaks up neatly with structure, the bimodal nature of *M. spicatum* could reflect the fine scale of its leaflets (size class -3 or -2) and the thicker size of its stems (size class 2). The fauna on *H. verticillata* tends towards one strong peak (size class 2 or 3) probably reflecting its leaflets and stems being about these sizes. Abundance values for the fauna on *V. americana* only show a peak at the smallest of scales, possibly reflecting that the broad flat blades cannot support abundant medium sized prey. The biomass plots reveal that *V. americana* supports a lot of biomass at the largest scales possibly in the predation shadow of its blades.

So linear regions of structure tend to be associated with abundance or biomass peaks at the large end of their range of scales. The way that complex regions affect

predation pressure and resulting prey peaks is still unclear. Hypothetically, a slight increase in complexity would probably still show the peaks, but a complex surface results in a prey item sacrificing a great deal of detectability and accessibility in order to outgrow some predators. The result should be that the peak in numbers does not reach the large end of the complex region but is displaced back towards smaller sizes by predation. Depending on the nature of the predators, a broad scale of high complexity may lead to several peaks spaced at intervals over the size classes. This is possibly why the number of abundance peaks found tended to correlate with overall plant complexity, and why they tended to be regularly spaced. The spacing itself might be indicative of the intensity of predation in conjunction with plant complexity.

A disputed contention in ecology is that differences in body mass allow different species to coexist by reducing competition. From this point of view, regular size differences imply that a minimum size difference is essential to maintain stable coexistence (Enders 1976; Bowers and Brown 1982; and Dickman 1988). Other workers contend that perceived regularity is no different than that expected from chance (Roth 1981; and Simberloff and Boecklen 1981), that competition is of little importance in maintaining these differences (Wiens 1982), or that other factors have at least as much impact (Dunham *et al.* 1978; and Simberloff 1984). Ricklefs *et al.* (1981) made nine structural measurements of 83 species of lizards from three different continents. They were able to demonstrate that the lizards of each continent occupied a unique morphological space, but the relation to ecological data was weak, leading the authors to state that for lizard communities, measurements of ecology and morphology provided different views of community structure, which overlap to an unknown extent. Tonkyn

and Cole (1986) conclude that size ratios do not have much predictive power to explain patterns of community membership.

This is not to say that regular spacing and the clumps of species with similar body masses might not be reflective of the dynamic between predation and competition. Imagine predation to be a constant with larger body size leading to increased vulnerability. Two similar species (A and B) feeding on the same resource would need to be far apart in body size. Since the larger species (A) feeds more efficiently, the smaller species (B) could coexist with the larger one by reducing its vulnerability to predation. In other words, B needs to be much smaller and/or exist in lower number than A. Now envision another food item utilized by a third species (C), which has a totally different feeding efficiency function. If species C is similar in size to species A and otherwise equally palatable, then it will draw predation away from A, further reducing B's ability to coexist. If C is similar in size to B, then the numbers of C can shoot up high since it is less visible than A and it has access to similar levels (albeit different types) of food. Body mass clumps appear to depend on the scaling of the food resources and the level of predation.

This dynamic could create an uneven distribution in prey sizes even if uncomplicated by structure in the habitat. Theoretically, structure would only help to enhance the clumping of the prey by creating differentials in overall vulnerability leading to unequal changes in the diet of predators. One of these changes that has been examined is diet breadth. Overall there has been contradictory evidence on the effect structure has on the diet breadths of fish predators. Two possibilities have been suggested as causing this contradiction. If the structure has the effect of decreasing the encounter rates, then

diet breadth should go up as was found by Vince *et al.* (1976) and others. Alternatively, if the change in encounter rate was not uniform but specific to the species of prey then a given species may be encountered much more frequently in the structured environment and thus potentially become specialized prey (Stoner 1982). Anderson (1984) examined these possibilities for largemouth bass feeding in either sparse vegetation or dense vegetation. He found some evidence that the encounter rate did change differentially, but that overall diet breadth increased in densely structured habitat.

The investigation of the body mass distribution of the fauna on plastic plant forms does reveal a clumped distribution, with the number and placement of these clumps being influenced by the form of the plants. However, clumps could not be correlated with specific plant structures or scaling regions. This, combined with an abundant distribution of periphyton, suggests that resource distribution *sensu* Holling (1992) was an unlikely explanation for the community structure. However, resource distribution may impact in conjunction with some other selective force such as predation, to produce the observed clumped distributions of body mass.

Alternative Explanations

The first two parts of this study turned out well. The opinion survey experiment provided strong evidence that the Richardson effect was a real phenomenon and not an artifact of measurement. The possibility exists that the box-counting plots were correlating with mean public opinion strictly through coincidence. Public opinion may have been based on some aspect of the images that we did not measure which happened to coincide with the Richardson effect. While this can certainly not be ruled out, it is unlikely that 12 images would coincide to that degree. Mean slope of the box-counting

plot was a powerful predictor of mean human response. This indicates that humans perceive the relativity of length to scale as complexity even if they do not consciously recognize it as such.

One may argue that human visual perception has nothing to do with a fish's physical access to a prey item. This is true, but it misses the point of the psychophysical experiment, which was not to link human perception to fish predation, but rather to prove that the Richardson effect was biologically real and that animals (in this case humans) respond to it. Note that mean overall complexity was not used again in the following experiments. A new set of experiments that sought to find out the relationship between predation and habitat complexity was conducted under the assumption that the Richardson effect was real, did measure complexity, and could be measured using the three axioms.

These experiments operated under the assumption that detectability and accessibility were functions of the plant surface. Furthermore, they operated under the assumption that detectability and accessibility were related functions of the plant surface. It was not possible to separate them within the framework of these experiments and it is possible that they confounded each other. Additionally, the detailed behavior of the fish as they responded to cover was not observed. It is possible that changing plant type led to behavioral changes. In that case, the responses measured may have been psychological phenomena of the fish instead of physical properties of the plant. Even staying within the physical properties of the plant, it is possible that some other nonlinear response of the fish was in action. For instance, the act of swimming in and around the plant may have resulted in a Richardson effect with changes in fish size. Heck and Orth

(1980) suggested that one could rank the amount of protection provided by an equal biomass of individual plant species based on their surface area per weight ratios. Of course surface area is just another linear measure and surely would have demonstrated the Richardson effect if it had been measured over several scales.

Good predictive power was shown by the working model and part two of this study ended with reasonable confidence in the assumptions. Part three, the effects on the community experiments, produced much more subjective results. These results, while consistent with the interaction between predator and prey being influenced by structure as a causative factor, were not conclusive. This left the possibilities of alternative explanations, such as the possibilities of random chance. Complex multi-peaked graphs are notoriously difficult to separate from random chance, especially when one is considering the sample unit to be a subset of such a distribution. The main difficulty in testing for this possibility lies in choosing a good null model, randomly selecting a population there from, and coming up with a workable statistic of similarity in order to find out if the samples are any less or more similar than those from nature.

One can also not rule out the possibility that the animals are on those particular plant forms because of choice rather than differential predation. The literature has numerous papers showing invertebrates actively choosing plant forms. By way of example, Hacker and Steneck (1990) made size comparisons of an amphipod on different forms. Their comparisons were somewhat similar to the current results, but they found that choice, not predation determined this. Of course, most authors acknowledge predator avoidance as an ultimate reason for this behavior to be considered adaptive.

Abiotic factors can create pattern in a community as well. Janzen and Schoener (1968) took sweep-net samples along a gradient of increasing length of rainy season in Costa Rica. As characteristic vegetation also changed along the gradient, it becomes impossible to separate plant structure effects from abiotic conditions. Having said this, with increasing rain comes increased vegetation structure and increased numbers of insects. The proportion of smaller insects also increases. This should not be a factor in an aquatic habitat, but something similar could be. It is not unreasonable to think of some factor, such as water depth, impacting the structure of the aquatic plants as well as the distribution of aquatic arthropods.

Abiotic effects can also interfere in a situation where predation is known to be a shaping factor. Stoner (1982) performed aquarium experiments that suggested amphipods would be less subject to predation from pinfish if they remained in *Thalassia* seagrass beds rather than *Halodule* beds. In a field experiment, Nelson (1980) found amphipod densities higher in *Halodule* in apparent contradiction to Stoner's work. Nelson suggested that the shallow waters of his *Halodule* site (25 cm) allowed the temperature to rise up to 34° C, which could have excluded a lot of fish predation. His *Thalassia* site was deeper (1.0 m) and cooler (29° C).

Habitat fragmentation can lead to clumped distributions of animals. With and Crist (1995) found that there is a critical threshold of percent cover. If the preferred habitat exceeds this threshold, then the animals will be randomly dispersed through the habitat. If on the other hand, the preferred habitat is less than the threshold, the animals will be aggregated. The value of the threshold depends on whether the animal is a generalist versus specialist, as well as its dispersal ability. Larger species are more likely

to be aggregated since they can survey more of the habitat and determine where the preferred habitat is. This model seemed to hold for grasshoppers in short-grass prairie in Colorado.

Even if pattern exists because of predation, there are reasons that parts of the pattern could be hidden or exaggerated. Price *et al.* (1980) presented the idea that if the plant material were rare or present for a short time, the plant would be under intense selective pressure to be toxic and thus likely to require a highly specialized herbivore. The result would be that for most of the time, it could avoid being detected and be relatively free of herbivores. When herbivores do find it, they are unlikely to encounter predators and can explode in number. When predators do finally find them, their numbers plummet. This boom and bust dynamics of herbivores and predators would mask plant structural effects. Any effect that predation would have on the herbivore community will need to be investigated at a large community level scale. If a plant species forms a long-term dominant part of the habitat, then the boom and bust of chance discoveries is reduced. Even if the plants are toxic, there is a near certain chance that they will be discovered by suitable herbivores which will in turn be discovered by suitable predators. Predator impacts are therefore most likely to be observed in large long lasting patches of vegetation. I stress here that predatory impacts should occur on all plant surfaces but that they will be most easily observed on large, long lasting patches of vegetation.

Plants can affect their arthropod communities by impacting on the recruitment of new immigrants or encouraging emigration. For example, Orr and Resh (1992) found that the plant *Myriophyllum aquaticum* affects recruitment of *Anopheles* mosquitoes. Lab

studies showed that oviposition rates increased with increasing plant stem density up to densities of 1,000 stems m^{-2} and then slowly decreased as densities approached 2,000 stems m^{-2} .

The community being observed might not yet be at equilibrium and therefore not accurately represent the relationship between predation and surface. A given community might never reach equilibrium but might be continuously reset through some catastrophic event. Dayton (1971) examined an interesting system where competition for space is moderated by predation and being constantly reset by physical disturbance. The system is the rocky shores of Washington and the physical disturbance comes from wave action and the battering effect of floating logs. On any clear space, barnacles are dominant competitors over algae. Once either barnacles or algae settle an area, then mussels settle in and displace the other two. Limpets hinder colonization by both barnacles and algae. Predatory gastropods selectively hinder some species of barnacle but when present with limpets will hinder all species of barnacle. One species of barnacle and the mussels have a growth escape from gastropod predation, but both are subject to predation from an asteroid *Pisaster ochraceus* (Brandt). So limpets and gastropods together control which species will dominate an area, but the actions of *Pisaster* and the impact from floating logs continually resets a resource limited area and allows the coexistence of all.

Equilibrium is normally thought of as a smooth distribution. Hicks (1980) compared the cumulative percentage of species versus the number of species divided into $\log_2$ size classes. A lognormal model would be a straight line that was taken to resemble the situation of a community in equilibrium, where immigrants balance emigrants. Departures from such a straight line would represent points of nonconformity and thus

represent communities out of equilibrium. He examined copepod assemblages on eight different algal species at two different sites. While plant complexity did not correlate with equilibrium, all sites in turbid water did appear to be out of equilibrium. In addition, two algal species are considered as fairly ephemeral in nature and their plots also appeared to be out of equilibrium

Time scales can be important in suppressing or revealing pattern. Edgar (1994) found a strong linear relationship between log sieve size and log abundance of marine macrofauna. Previous studies found polymodal relationships over larger scales (Schwinghamer 1981, 1985, Edgar *et al.* 1994). A possible explanation arose from the fact that any variations from linearity in his study involved animals greater than 5.6 mm diameter and greater than 1 year in age. It was suggested that size-dominance studies might only be useful for fauna less than a given size. This would ensure that the community size-structure observed reflected recent influences like predation and competition. If larger animals are included, the size-structure begins to reflect major past events such as inter-annual variation in recruitment

Time, succession, and catastrophes can all interact with the specific adaptations of individual species resulting in once favorable size classes becoming maladapted. Black and Hairston (1988) examined the microcrustacean zooplankton of a small pond in Rhode Island. For the first two years of the study, the dominant predator was the redbreast sunfish, *Lepomis auritus* (L.). Higher temperatures and lower pond volume led to peak predation pressure occurring in the middle of the summer months. This resulted in a noticeable decrease in the largest prey size classes. The pond dried completely in the third year, which eliminated all the fish. The predatory midge *Chaoborus americanus*

(Johannsen) rapidly colonized the pond. This species is strictly univoltine in the area, so all predators started out in the spring as small in size. This made it possible for prey species to escape predation by outgrowing the predator. As the season progressed and the midge molted, the prey needed to grow bigger and bigger to escape predation. Eventually, they were unable to outgrow the midge and the large prey size classes dropped to near zero. The end result is that the temporal pattern of large prey size class peaked in the summer when midges were the main predators and in the winter when fish were the main predators. The summer abundance of large prey items could occur only when the prey were able to outgrow the predatory midges and remove themselves from the equation. Once they were unable to do that (i.e., late summer), their numbers reverted to that of being under fish predation. Of the twelve species examined during the study, only one became less common when midges were the predators. In other words, less predation on large prey items was not complemented by increased predation on small prey items. The only exception was one copepod species. This middle to large sized species was particularly adapted to survive fish predation. It survives the summer as aestivating eggs that hatch in the fall. It therefore is not present when fish predation is highest. Unfortunately, this strategy makes it present at just the time when midge predation is the highest. This specific adaptation allowed an otherwise vulnerable prey item to survive a specific predator but this adaptation became a handicap when a different predator became abundant.

Something as simple as your sampling strategy could also affect your results. Taylor *et al.* (1984) compared stratified random versus systematic sampling strategies and how they affected correlation between various fauna and floral aspects of northern

Australia. If stratified random sampling was chosen, then most of the fauna correlated with vegetation structure and life form. Systematic sampling could include ecotones and thus always included more species than stratified random sampling. Also, fauna correlated more closely with floristics rather than structure when systematic sampling was employed. Choosing stratified samples that are too far away may make a continuum appear disjoint. Of course this does not preclude the idea that distributions may be both continuous and disjoint. The question is one of scale. Distribution within a sampling site may be structure determined but distribution across larger scales may be floristic.

Cross-scale phenomena occurring simultaneously have been observed before. Huntsman (1979) saw the fish community of a coral reef as arising from a fusion of behavioral, physiological, and morphological factors all impacting on the interaction between predator and prey, which through evolutionary time determines which behavioral, physiological, and morphological factors arise. In essence, Huntsman describes a co-evolutionary cycle, which can be divided into coarse and fine grains. Coarse grain structure is related to the higher order taxonomic levels and broad-scaled generalistic behaviors while fine-scaled structure is related to species level distinctions and microniche separations. He saw adaptations to the coarse grain as a direct result of predation pressure while fine grain adaptations were the result of competition. For example, schooling is usually considered a response to predation pressure yet a whole guild of species will utilize this behavior at any given place or time. The determination of what species are present is a function of the competition within the guild. To simplify, predation determines the relative abundance of guilds while competition determines the relative abundance of species within a guild.

Karban (1989) studied three different herbivorous insects attacking leaves of the Seaside Daisy, *Erigeron glaucus* Ker-Gawl. Each of the insect species was controlled by a different limiting factor with no significant interaction between them. Plume moth caterpillars were controlled primarily by the actions of insectivorous sparrows. Spittlebugs were controlled by predation from the caterpillars in that caterpillar-damaged leaves caused the spittlebugs to desiccate. Thrips seemed to be controlled by the clonal variety of plant and the weather. The author developed a hierarchical concept of the controlling factors. If predation and parasitism are intense, then competition and plant variety have little effect. In the absence of significant predation, competition will determine the dynamics. In the absence of other controlling factors, plant variety and weather play dominant roles. This is a classic hierarchical organization with predation, competition, and plant variety being the fast, middle, and slow cycle, respectively.

Future Research

There is a great deal that still needs to be accomplished before we reach the point of fully understanding the relationship between shape, predation, and the success of species. Even the basics of shape and box-counting can not be considered as fully known. For one thing, this work condensed all forms into two-dimensional representations. Sadly, three-dimensional imaging is not yet usable in a form capable of supporting cube-counting. Until computer technology catches up, box-counting will have to stay. However, one can consider the changes in box-counting plots over time with current technologies. Also, satellite technology allows box-counting and ecology to interact over huge scales.

Basic work on predation also needs to progress. The entire concept of the effect of shape on the functional response should prove to be a fruitful field of research. Density is of course the fundamental concept behind functional response, but should density be determined at the level of the predator or of the prey? That has large implications for the number and distribution of predators supportable by prey on a complex surface. Different types of predators should be examined as well. The metabolic makeup of the predator could be considered as well as the mode of eating. Do predators that engulf their prey intact perceive the same levels of accessibility? Does the search pattern change with plant complexity? Do ambush hunters reflect the interaction of complexity with the predator or with the prey? Which hunting style produces the best results on a given level of complexity?

Prey characteristics can also be investigated as adaptations to plant complexity. Can prey camouflage be quantified or predicted? Does behavior such as swarming or foraging path interact with shape? Does complexity impact on the size and number of offspring of a prey species? Competition on a complex surface might also prove enlightening. Indeed, the question of the responses of individual guilds to complexity should prove interesting.

Perhaps an even greater field of information can be gleamed from consideration of the plant's point of view. Is a particular growth form a response to increase the vulnerability of herbivorous insects? Are some levels of complexity designed to give cover to medium sized predators of herbivorous insects? The idea of a particular plant form interacting with a preexisting population of arthropods might help to explain why

some plants are invasive. Can the arthropod populations on invasive weeds be looked at for the purpose of identifying "under utilized" niches?

By no means should this work be considered the definitive work on the use of complexity (fractal or otherwise) in ecological research. As the above handful of questions reveal, only the surface has been scratched and a great deal is yet to be learned. Hopefully, this work has pointed the direction for continuing research in nonlinear ecologies involving shape, predation, and community structure.

APPENDIX

MATLAB LANGUAGE COMPUTER PROGRAMS

Program 1. boco.m

```
%function boco
% This function imports a PCX file where all pixels within the object
have a value greater than 1, and presents a box-counting plot across
scale. The output is two vectors of equal length; S, the scale of
measurement from 1 to 300 pixels (expressed in mm), and N, the number
of grids intersected by the edge of the object at each scale
% This function requires the function yne.m
fname = input('Enter PCX picture file name ','s');
[x,map] = pcxread(fname);
res = input('At what resolution (dpi) was the image scanned? ');
[H L] = size(x);
pp = figure
S = []; N = []; XX = []; YY = [];
%
X = x - 1;
iX = find(X>0);
X(iX) = ones(size(iX));
YY = nlfilter(X,[3 3],'yne');
%
for pX = 1:300
    s = (pX * 25.4)/res;
    S = [S s];
    if pX == 1
        nn = length(find(YY));
    else
        r = ceil(H/pX);
        c = ceil(L/pX);
        XX = zeros(r,c);
        for R = 1:r
            for C = 1:c
                if R == 1
                    brow = 1;
                else
                    brow = ((R-1)*pX) + 1;
                end
                if R == r
                    erow = H;
                else
                    erow = R * pX;
                end
                if C == 1
                    bcol = 1;
                else
                    bcol = ((C-1)*pX) + 1;
                end
                if C == c
```

```

        ecol = L;
    else
        ecol = C * pX;
    end

    my = mean2(YY(brow:erow,bcol:ecol));
    if my > 0
        XX(R,C) = 1;
    else
        XX(R,C) = 0;
    end
end
end
end
nn = length(find(XX));
N = [N nn];
end

figure
loglog(S,N,'y-')
title('Box-counting Plot')
xlabel('log scale of measurement (mm)')
ylabel('log count')

```

PROGRAM 2. yne.m

```

function y = yne(x)
%yes or no binary edge, to be used as a non-linear filter for the
program boco.m
%This program takes a 3 x 3 binary matrix and determines whether the
center value is part of the edge of the object (value = 1) or not
(value = 0).

if x(2,2) == 0
    y = 0;
else
    xx = mean2(x);
    if xx == 0
        y = 0;
    elseif xx == 1
        y = 0;
    else
        y = 1;
    end
end
end

```

REFERENCES

- Abele, L.G. 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology* 55: 156-161.
- Addicott, J.F. 1974. Predation and prey community structure: An experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. *Ecology* 55: 475-492.
- Allen, J.C., and D. Gonzalez. 1975. The effects of temperature and host refuge on insect host-parasite models. *Environ. Entomol.* 4: 57-65.
- Ambrose, R.F. and T.W. Anderson. 1990. Influence of an artificial reef on the surrounding infaunal community. *Mar. Biol. (Berlin)* 107: 41-52.
- Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65: 851-861.
- Anderson, T.W. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar. Ecol. Prog. Ser.* 113: 279-290.
- Andow, D.A. and D.R. Prokrym. 1990. Plant structural complexity and host-finding by a parasitoid. *Oecologia* 82: 162-165.
- Angermeier, P.L. and I.J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70: 1450-1462.
- Arthur, A.P. 1962. Influence of host tree on abundance of *Itopectis conquisitor* (Say) (Hymenoptera: Ichneumonidae), a polyphagous parasite of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *Can. Entomol.* 94: 337-347.
- Askew, R.R. 1961. On the biology of the inhabitants of oak gall of Cynipidae (Hymenoptera) in Britain. *Trans. Soc. Brit. Entomol.* 14: 237-68.
- Askew, R.R. and J.M. Ruse. 1974. The biology of some Cecidomyiidae (Diptera) galling the leaves of birch (*Betula*) with special reference to their chalcidoid (Hymenoptera) parasites. *Trans. R. Entomol. Soc. London* 126: 129-67.
- August, P.V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64: 1495-1507.

- Baelde, P. 1990. Differences in the structures of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. *Mar. Biol.* 105: 163-173.
- Ball, J.C. and D.L. Dahlsten. 1973. Hymenopterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contribution to mortality. I. Influence of host tree and tree diameter on parasitization. *Can. Entomol.* 105: 1453-64.
- Barkai, A., and C. McQuaid. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* 242: 62-64.
- Basset, Y., R.L. Kitching. 1991. Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecol. Entomol.* 16: 391-402.
- Bazzaz, F.A. 1975. Plant species diversity in old field successional ecosystems in southern Illinois. *Ecology* 56: 485-488.
- Beckett, D.C., T.P. Aartila, and A.C. Miller. 1992. Invertebrate abundance on *Potamogeton nodosus*: effects of plant surface area and condition. *Can. J. Zool.* 70: 300-306.
- Beier, P. and J.E. Drennan. 1997. Forest structure and prey abundance in foraging areas of northern goshawks. *Ecol. Appl.* 7: 564-571.
- Bell, S.S. 1985. Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage. *J. Mar. Res.* 43: 647-672.
- Bell, S.S. and S.A. Woodin. 1984. Community unity: experimental evidence for macrofauna and meiofauna. *J. Mar. Res.* 42: 605-632.
- Benson, B.J. and J.J. Magnuson. 1992. Spatial heterogeneity of littoral fish assemblages in lakes: Relation to species diversity and habitat structure. *Canad. J. Fish. Aquat. Sci.* 49: 1493-1500.
- Bequaert, J. 1924. Galls that secrete honeydew. A contribution to the problem as to whether galls are altruistic adaptations. *Bull. Brooklyn Entomol. Soc.* 19: 101-24.
- Berntson, G.M. 1994. Root systems and fractals: how reliable are calculations of fractal dimensions. *Ann. Bot.* 73: 281-284.
- Bettoli, P.W., M.J. Maceina, R.L. Noble and R.K. Betsill. 1992. Piscivory in largemouth bass as a function of aquatic vegetation abundance. *N. Amer. J. Fish. Manage.* 12: 509-516.

- Black, R.W., II, and N.G. Hairston, Jr. 1988. Predator driven changes in community structure. 1988. *Oecologia* 77: 468-479.
- Blaustein, L, B.P. Kotler, and D. Ward. 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary ponds. *Ecol. Entomol.* 20: 311-318.
- Bolton, R.G., and L. Boddy. 1993. Characterization of the spatial aspects of foraging mycelial cord systems using fractal geometry. *Mycol. Res.* 97: 762-768.
- Bowers, M.A., and J.H. Brown. 1982. Body size and co-existence in desert rodents: Chance or community structure? *Ecology* 63: 391-400.
- Brett, M.T. 1992. *Chaoborus* and fish-mediated influences on *Daphnia longispina* population structure, dynamics and life history strategies. *Oecologia* 89: 69-77.
- Bridwell, J.C. 1918. Notes on the Bruchidae and their parasites in the Hawaiian Islands. *Proc. Hawaiian Entomol. Soc.* 3: 465-505.
- Bridwell, J.C. 1920. Notes on the Bruchidae and their parasites in the Hawaiian Islands. 3rd Paper. *Proc. Hawaiian Entomol. Soc.* 4: 403-9.
- Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. *Science*, N.Y. 150: 28-35.
- Brown, J.H. and B.A. Maurer. 1986. Body size, ecological dominance and Cope's rule. *Nature* 324: 248-250.
- Bruce, V., P.R. Green, and M.A. Georgeson. 1997. **Visual Perception; Physiology, Psychology, and Ecology, 3rd Ed.** Psychology Press, Hove, UK.
- Butler, J.J., IV 1989. Community responses to variable predation: Field studies with sunfish and freshwater macroinvertebrates. *Ecol. Monogr.* 59: 311-328.
- Caley, M.J. and J. St. John. 1996. Refuge availability structures assemblages of tropical reef fishes. *J. Animal Ecol.* 65: 414-428.
- Cárcamo, H.A., and J.R. Spence. 1994. Crop type effects on the activity and distribution of ground beetles (Coleoptera: Carabidae). *Environ. Entomol.* 23: 684-692.
- Charnov, E.L. 1976. Optimal foraging; attack strategy of a mantid. *Amer. Natural.* 110: 141-151.
- Chilton, E.W. and F.J. Margraf. 1990. Effects of fish predation on invertebrates associated with a macrophyte in Lake Onalaska, Wisconsin. *J. Freshwat. Ecol.* 5: 289-296.

- Chiravathanapong, S.N., and H.N. Pitre. 1980. Effects of *Heliothis virescens* larval size on predation by *Geocoris punctipes*. Fla. Entomol. 63: 146-151.
- Choat, J.H. and A.M. Ayling. 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. J. Exper. Mar. Biol. Ecol. 110: 257-284.
- Clarke, K.R. 1990. Comparison of dominance curves. J. Exp. Mar. Biol. Ecol. 138: 143-157.
- Cloarec, A. 1990. Factors influencing the choice of predatory tactics in a water bug, *Diplonychus indicus* Venk. and Rao (Heteroptera: Belostaomatidae). Anim. Behav. 40: 262-271.
- Cody, M.L. 1968. On the methods of resource subdivision in grassland bird communities. Amer. Natural. 102: 107-147.
- Coen, L.D., K.L. Heck, Jr., and L.G. Abele. 1981. Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62: 1484-1493.
- Collings, J.B. 1995. Bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge. Bull. Math. Biol. 57: 63-76.
- Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monog. 40: 49-78.
- Cooper, W.E., and L.B. Crowder. 1979. Patterns of predation in simple and complex environments. In **Predator-Prey Systems in Fisheries Management**. R.H. Stroud and H. Clepper, Eds., Sport Fishing Institute, Washington, DC Pp. 257-267.
- Coull, B.C., and J.B.J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64: 1599-1609.
- Crowder, L.B., and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.
- Cutting, J.E., and J.J. Garvin. 1987. Fractal curves and complexity. Percep. Psychophys. 42: 365-370.
- Damuth, J. 1981. Population density and body size in mammals. Nature 290: 699-700.
- Darlington, A. 1975. **The Pocket Encyclopaedia of Plant Galls in Colour**, rev. Ed. Poole, Dorset: Blandford.

- Dayton, P.K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.
- Dean, R.L., and J.H. Connell. 1987a. Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. *J. Exp. Marine Biol. Ecol.* 109: 195-215. .
- Dean, R.L., and J.H. Connell. 1987b. Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. *J. Exp. Marine Biol. Ecol.* 109: 217-247.
- Dean, R.L., and J.H. Connell. 1987c. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *J. Exp. Marine Biol. Ecol.* 109: 249-273.
- DeBach, P., and D. Rosen. 1991. **Biological Control by Natural Enemies**, 2nd Ed. Cambridge University Press, New York, NY.
- DeVries, D.R. 1990. Habitat use by bluegill in laboratory pools: Where is the refuge when macrophytes are sparse and alternative prey are present? *Environ. Biol. Fishes* 29: 27-34.
- Dibble, E.D., K.J. Killgore, and Harrel. 1997. Assessment of fish-plant interactions. Misc. Paper a-97-6, U.S. Army Eng. Waterways Exp. Stn. Vicksburg, MS.
- Dickman, C.R. 1988. Body size, prey size, and community structure in insectivorous mammals. *Ecology* 69: 569-580.
- Diehl, S. 1992. Fish predation and benthic community structure: The role of omnivory and habitat complexity. *Ecology* 73: 1646-1661.
- Dionne, M., and C.L. Folt. 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. *Can. J. Fish. Aquat. Sci.* 48: 123-131.
- Dittrich, W., F.S. Gilbert, P.R. Green, P.K. McGregor, and D. Grewcock. 1993. Imperfect mimicry: A pigeon's perspective. *Proc. R. Soc. Lond. B.* 251: 195-200.
- Döbel, H.G., R.F. Denno and J.A. Coddington. 1990. Spider (Araneae) community structure in an intertidal salt marsh: Effects of vegetation structure and tidal flooding. *Environ. Entomol.* 19: 1356-1370.
- Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.* 15: 131-137.

- Dowden, P.B., V.M. Carolin, and C.O. Dirks. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946-1948. *J. Econ. Entomol.* 43: 774-83.
- Downes, B.J., P.S. Lake, and E.S.G. Schreiber. 1995. Habitat structure and invertebrate assemblages on stream stones: A multivariate view from the riffle. *Austral. J. Ecol.* 20: 502-514.
- Dunham, A.E., D.W. Tinkle, and J.W. Gibbons. 1978. Body size in island lizards: a cautionary tale. *Ecology* 59: 1230-1238.
- Edgar, G.J. 1994. Observations on the size-structure of macrofaunal assemblages. *J. Exper. Mar. Biol. Ecol.* 176: 227-243.
- Edgar, G.J. and A.I. Robertson. 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: Pattern and process in a western Australian *Amphibolis* bed. *J. Exper. Mar. Biol. Ecol.* 160: 13-31.
- Edgar, G.J., C. Shaw, G.F. Watson and L.S. Hammond. 1994. Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *J. Exp. Mar. Biol. Ecol.* 176: 201-206.
- Eghball, B., J.R. Settimi, J.W. Maranville, and A.M. Parkhurst. 1993. Fractal analysis for morphological description of corn roots under nitrogen stress. *Agron. J.* 85: 287-289.
- Ekbom, B.S. 1977. Development of a biological control program for greenhouse whiteflies (*Trialeurodes vaporarum* Westwood) using its parasite (*Encarsia formosa* (Gahan) in Sweden. *Z. Angew. Entomol.* 84: 145-54.
- Elsay, K.D. 1974. Influence of plant host on searching speed of two predators. *Entomophaga* 19: 3-6.
- Elvin, M.K., J.L. Stimac, and W.H. Whitcomb. 1983. Estimating rates of arthropod predation of velvetbean caterpillar larvae in soybeans. *Fla. Entomol.* 66: 319-330.
- Emlen, J.M. 1966. The role of time and energy in food preference. *Amer. Natural.* 100: 611-617.
- Enders, F. 1976. Size, food-finding, and Dyar's constant. *Environ. Entomol.* 5: 1-10.
- Erwin, T.L. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. *In. Tropical Rain Forest: Ecology and Management.* S.L. Sutton, T.C. Whitmore and A.C. Chadwick, Eds., Special publication no. 2, British Ecol. Soc. Blackwell, Oxford. Pp. 59-75.

- Erwin, T.L. and J.C. Scott. 1980. Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Lucea seemanii* Triana and Planch in the Canal Zone of Panama. *Coleop. Bull.* 34: 305-322.
- Etnier, D.A., and W.C. Starnes. 1993. **The Fishes of Tennessee**. The University of Tennessee Press, Knoxville, TN.
- Evans, H.F. 1976a. The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrtosiphon pisum*. *Ecol. Entomol.* 1: 85-90.
- Evans, H.F. 1976b. The searching behaviour of *Antocoris confusus* (Reuter) in relation to prey density and plant surface topography. *Ecol. Entomol.* 1: 163-69.
- Evans, L.J. and R.H. Norris. 1997. Prediction of benthic macroinvertebrate composition using microhabitat characteristics derived from stereo photography. *Freshwat. Biol.* 37: 621-633.
- Fagan, W.F. and L.E. Hurd. 1991. Direct and indirect effects of generalist predators on a terrestrial arthropod community. *Amer. Midl. Natural.* 126: 380-384.
- Fagan, W.F. and L.E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: Population consequences and community impact. *Ecology* 75: 2022-2032.
- Fitter, A.H., and T.R. Stickland. 1992. Fractal characterization of root system architecture. *Funct. Ecol.* 6: 632-635.
- Flecker, A.S. 1992. Fish trophic guilds and the structure of a tropical stream: Weak direct vs. strong indirect effects. *Ecology* 73: 927-940.
- Formanowicz, D.R., Jr. 1987. Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): Prey detection, reactive distance and predator size. *J. Kans. Entomol. Soc.* 60: 92-99.
- Fowler, S.V. 1985. Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: The importance of plant architecture. *Ecol. Entomol.* 10: 159-169.
- Francis, D.R. and T.C. Kane. 1995. Effect of substrate on colonization of experimental ponds by Chironomidae (Diptera). *J. Freshwat. Ecol.* 10: 57-63.
- Frazer, B.D. and R.R. McGregor. 1994. Searching behaviour of adult female Coccinellidae (Coleoptera) on stem and leaf models. *Can. Entomol.* 126: 389-399.

- Fretwell, S.D. 1977. The regulation of plant communities by food chains exploiting them. *Persp. Biol. Med.* 20: 169-185.
- Fretwell, S.D. 1987. Food chain dynamics: The central theory of Ecology? *Oikos* 50: 291-301.
- Galbraith, Jr., M.G. 1967. Size selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96: 1-10.
- Gardner, S.M., and A.F. G. Dixon. 1985. Plant structure and the foraging success of *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). *Ecol. Entomol.* 10: 171-179.
- Garvey, J.E., R.A. Stein, and H.M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* 75: 532-547.
- Gause, G.F. 1934. **The Struggle for Existence**. Hafner, NY. (Reprinted 1964)
- Gerking, S.D. 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38: 219-225.
- Gibbons, M.J. 1988. The impact of sediment accumulations, relative habitat complexity and elevation on rocky shore meiofauna. *J. Exper. Mar. Biol. Ecol.* 122: 225-242.
- Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65: 455-468.
- Glass, N.R. 1971. Computer analysis of predation energetics in the largemouth bass. *In: Systems Analysis and Simulation in Ecology, Vol. 1*, B.C. Patten, Ed., Academic Press, New York, NY. Pp. 325-363.
- Goldstein, E.B. 1989. **Sensation and Perception, 3rd Ed.** Wadsworth Publishing Co., Belmont, CA.
- Graham, S.A., and L. G. Baumhofer. 1927. The pine tip moth in the Nebraska National Forest. *J. Agric. Res.* 35: 323-33.
- Gregg, W.W. and F.L. Rose. 1985. Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia* 128: 45-56.
- Grevstad, F.S., and B.W. Klepetka. 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* 92: 399-404.
- Griffiths, D. 1980. Foraging costs and relative prey size. *Amer. Natural.* 116: 743-752.

- Griffiths, D. 1986. Size-abundance relations in communities. *Amer. Natural.* 127: 140-166.
- Gunnarsson, B. 1992. Fractal dimension of plants and body size distribution in spiders. *Funct. Ecol.* 6: 636-641.
- Hacker, S.D. and R.S. Steneck. 1990. Habitat architecture and the abundance and body-size dependent habitat selection of a phytal amphipod. *Ecology* 71: 2269-2285.
- Hairton, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. *Amer. Natural.* 94: 421-424.
- Hanson, J.M. 1990. Macroinvertebrate size-distribution of two contrasting fresh-water macrophyte communities. *Freshwat. Biol.* 24: 481-491.
- Hargeby, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos* 57: 338-346.
- Harvey, P.H. and J.H. Lawton. 1986. Patterns in three dimensions. *Nature* 324: 212.
- Haslett, J.R. 1994. Community structure and the fractal dimensions of mountain habitats. *J. Theor. Biol.* 167: 407-411.
- Hastings, H.M., and G. Sugihara. 1993. **Fractals: A User's Guide for the Natural Sciences.** Oxford University Press, New York, NY.
- Hawkins, B.A., M.B. Thomas, and M.E. Hochberg. 1993. Refuge theory and biological control. *Science* 262: 1429-1432.
- Haynes, D.L., and J.W. Butcher. 1962. Studies on host preference and its influence on European Pine Shoot Moth success and development. *Can. Entomol.* 94: 690-706.
- Heck, K.L., Jr. and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. *In. Estuarine Perspectives*, V.S. Kennedy, Ed., Academic Press, New York, NY.
- Heck, K.L., Jr. and G.S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J. Biogeogr.* 4: 135-142.
- Heimpel, G.E. and J.A. Hough-Goldstein. 1994. Components of the functional response of *Perillus bioculatus* (Hemiptera: Pentatomidae). *Environ. Entomol.* 23: 855-859.

- Hicks, G.R.F. 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *J. Exper. Marine Biol. Ecol.* 44: 157-192.
- Holling, C.S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* 6: 163-182.
- Holling, C.S. 1986. The resilience of terrestrial ecosystems, local surprise and global change. *In. Sustainable Development of the Biosphere*, W.C. Clark and R.E. Munn, Eds., Cambridge University Press, Cambridge, Pp. 292-317.
- Holling, C.S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecol. Monog.* 62: 447-502.
- Holling, C.S., G. Peterson, P. Marples, J. Sendzimir, K. Redford, L. Gunderson and D. Lambert. 1996. Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. *In. Global Change and Terrestrial Ecosystems*. B.H. Walker and W.L. Steffen, Eds. Cambridge University Press, Cambridge, Pp. 346-384.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions and the coexistence of prey species. *Amer. Natural.* 124: 377-406.
- Huey, R.B., and E.R. Pianka. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.
- Huffaker, C.B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia* 27: 343-383.
- Hulspas-Jordan, P.M. and J.C. van Lenteren. 1978. The relationship between host-plant leaf structure and parasitization efficiency of the parasitic wasp *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae). *Med. Fac. Landbouww. Rijksuniv. Gent* 43: 431-40.
- Huntsman, G.R. 1979. Predation's role in structuring reef fish communities. *In. Predator-Prey Systems in Fisheries Management*. R.H. Stroud and H. Clepper, Eds., Sport Fishing Institute, Washington, DC, Pp. 103-108.
- Hurd, L.E. and R.M. Eisenberg. 1990. Arthropod community responses to manipulation of a bitrophic predator guild. *Ecology* 71: 2107-2114.
- Hurd, L.E., and W.F. Fagan. 1992. Cursorial spiders and succession: Age or habitat structure. *Oecologia* 92: 215-221.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *Amer. Natural.* 93: 145-159.

- Hutchinson, G.E. and R.H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. *Amer. Natural.* 93: 117-125.
- Iribarne, O. 1996. Habitat structure, population abundance and the opportunity for selection on body weight in the amphipod *Eogammarus oclairi*. *Mar. Bio.* 127: 143-150.
- Jakobsen, P.J., and G.H. Johnsen. 1988. Size-specific protection predation by fish in swarming waterfleas, *Bosmina longispina*. *Anim. Behav.* 36: 986-990.
- Janzen, D.H. 1973. Sweep samples of tropical foliage insects: Description of study sites, with data on species abundances and size distributions. *Ecology* 54: 659-686.
- Janzen, D.H., and T.W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96-110.
- Juliano, S.A., and J.H. Lawton. 1990a. The relationship between competition and morphology. I. Morphological patterns among co-occurring dytiscid beetles. *J. Anim. Ecol.* 59: 403-419.
- Juliano, S.A., and J.H. Lawton. 1990b. The relationship between competition and morphology. II. Experiments on co-occurring dytiscid beetles. *J. Anim. Ecol.* 59: 831-848.
- Kampichler, C. 1993. Biomass distribution of a microarthropod community in spruce forest soil. *Biol. Fertil. Soils* 19: 263-265.
- Karban, R. 1989. Community organization of *Erigeron glaucus* folivores: Effects of competition, predation, and host plant. *Ecology* 70: 1028-1039.
- Kareiva, P. and R. Sahakian. 1990. Tritrophic effects of a simple architectural mutation in pea plants. *Nature* 345: 433-434.
- Katanyukul, W., and R. Thurston. 1973. Seasonal parasitism and predation of eggs of the tobacco hornworm on various host plants in Kentucky. *Environ. Entomol.* 2: 39-45.
- Kaye, B.H. 1989. **A Random Walk Through Fractal Dimensions**. VCH Publishers, New York, NY.
- Kelly, J.F. 1996. Effects of substrate on prey use by belted kingfishers (*Ceryle alcyon*): A test of the prey abundance-availability assumption. *Canad. J. Zool.* 74: 693-697.

- Kern, J.C. and G.L. Taghon. 1986. Can passive recruitment explain harpacticoid copepod distributions in relation to epibenthic structure? *J. Exper. Mar. Biol. Ecol.* 101: 1-24.
- Kettlewell, B. 1973. **The Evolution of Melanism.** Oxford University Press, Oxford, UK.
- Kohler, S.L. 1992. Competition and the structure of a benthic stream community. *Ecol. Monogr.* 62: 165-188.
- Kohn, A.J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *Amer. Natural.* 101: 251-259.
- Kohn, A.J., and P.J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* 25: 199-210.
- Kolasa, J. 1989. Ecological systems in hierarchical perspective: Breaks in community structure and other consequences. *Ecology* 70: 36-47.
- Kotzageorgis, G.C. and C.F. Mason. 1997. Small mammal populations in relation to hedgerow structure in an arable landscape. *J. Zool.* 242: 425-434.
- Krantz, G.W. 1978. **A Manual of Acarology, 2nd Ed.** Oregon State University Book Stores, Inc., Corvallis, OR.
- Krebs, J.R. 1978. 2. Optimal Foraging: decision rules for predators. *In: Behavioural Ecology; A Evolutionary Approach.* J.R. Krebs and N.B. Davies Eds., Blackwell Scientific Publications, Oxford. Pp. 23-63.
- Krecker, F.H. 1939. A comparative study of the animal populations of certain submerged aquatic plants. *Ecology* 20: 553-562.
- Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. *Ann. Rev. Entomol.* 28: 23-39.
- Lawton, J.H. 1986. Surface availability and insect community structure: The effects of architecture and fractal dimension of plants. *In Insects and the Plant Surface.* B.E. Juniper and T.R.E. Southwood, Eds., Edward Arnold, London, UK. Pp. 317-331.
- Lawton, J.H. 1990. Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. *Phil. Trans. R. Soc. Lond. B.* 330; 283-291.

- Lawton, J.H., J.R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. *In*. **Ecological Stability**. M.B. Usher and M.H. Williamson, Eds., Chapman and Hall Ltd., London, UK. Pp. 141-158.
- Leber, K.M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66: 1951-1964.
- Letourneau, D.K. 1990. Mechanisms of predator accumulation in a mixed crop system. *Ecol. Entomol.* 15: 63-69.
- Levin, D.A. 1973. The role of trichomes in plant defense. *Q. Rev. Biol.* 48: 3-15.
- Lewis, F.G. III. 1984. The distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule*, and bare sand substrata. *Mar. Ecol. Prog. Ser.* 19:101-113.
- Lipcius, R.N., and A.H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361-1371.
- Luckinbill, Y.S. 1973. Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*. *Ecology* 54: 1320-1327.
- Lynch, J., and J.J. van Beem. 1993. Growth and architecture of seedling roots of common bean genotypes. *Crop Sci.* 33: 1253-1257.
- Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. *Ecology* 58: 763-774.
- Lynch, W.E., Jr., and D.L. Johnson. 1989. Influences of interstice size, shade, and predators on the use of artificial structures by bluegills. *N. Amer. J. Fish. Manage.* 9: 219-255.
- Macan, T.T. 1976. A twenty-one year study of the water-bugs in a moorland fishpond. *J. Animal Ecol.* 45: 913-922.
- MacArthur, R.H. 1972. **Geographical Ecology**. Harper and Row, New York, NY.
- MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42: 594-598.
- MacArthur, R.H., J.W. MacArthur and J. Preer. 1962. On bird species diversity. II. Prediction of bird censuses from habitat measurements. *Amer. Natural.* 96: 167-174.
- MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. *Amer. Natural.* 100: 603-609.

- MacArthur, R.H., and E.O. Wilson. 1967. **The Theory of Island Biogeography**. Princeton University Press, Princeton, NJ.
- Main, K.L. 1987. Predator avoidance in seagrass meadows: Prey behavior, microhabitat selection, and cryptic coloration. *Ecology* 68: 170-180.
- Mandelbrot, B.B. 1963. The variation of certain speculative prices. *J. Business* (Chicago) 36: 394-419.
- Mandelbrot, B.B. 1965. Self similar error clusters in communications systems and the concept of conditional stationarity. *IEEE Tr. On Communications Technology* 13: 71-90.
- Mandelbrot, B.B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. *Science* 155: 636-638.
- Mandelbrot, B.B. 1983. **The Fractal Geometry of Nature**. W.H. Freeman and Co. New York, NY.
- Marinelli, R.L., and B.C. Coull. 1987. Structural complexity and juvenile fish predation on meiobenthos: an experimental approach. *J. Exp. Mar. Biol. Ecol.* 108: 67-81.
- Martin, T.H., L.B. Crowder, C.F. Dumas, and J.M. Burkholder. 1992. Indirect effects of fish on macrophytes in Bays Mountain Lake: Evidence for littoral trophic cascade. *Oecologia* 89: 476-481.
- Mason, R.R. 1992. Populations of arboreal spiders (Araneae) on Douglas-firs and true firs in the interior Pacific Northwest. *Environ. Entomol.* 21: 75-80.
- Maurer, B.A., and J.H. Brown. 1988. Distribution of energy use and biomass among species of North American terrestrial birds. *Ecology* 69: 1923-1932.
- May, R.M. 1975. Patterns of species abundance and diversity. *In. Ecology and Evolution of Communities*. M.L. Cody and J.M. Diamond, Eds., Harvard University Press, Cambridge, MA. Pp. 81-120.
- May, R.M. 1978. The dynamics and diversity of insect faunas. *In. Diversity of Insect Faunas*. L.A. Mound and N. Waloff, Eds., Symposia Royal Entomological Society of London 9, Blackwell Scientific Publications, Oxford, UK, Pp. 188-204.
- May, R.M. 1981. Patterns in Multi-Species Communities *In. Theoretical Ecology; Principles and Applications*, 2nd Ed. Blackwell, Oxford, UK, Pp. 197-227.
- May, R.M. 1986. The search for patterns in the balance of nature: Advance and retreats. *Ecology* 67: 1115-1126.

- Maynard Smith, J. 1974. **Models in Ecology**. Cambridge University Press, Cambridge, UK.
- McArdle, B.H., and J.H. Lawton. 1979. Effects of prey-size and predator-instar on the predation of *Daphnia* by *Notonecta*. *Ecol. Entomol.* 4: 267-275.
- McLellan, T., and J.A. Endler. 1998. The relative success of some methods for measuring and describing the shape of complex objects. *Syst. Biol.* 47: 264-281.
- McNair, J.N. 1986. The effects of refuges on predator-prey interactions: a reconsideration. *Theor. Pop. Biol.* 29: 38-63.
- Meisch, M.V. 1985. Chapter 2. *Gambusia affinis affinis*. In. **Biological Control of Mosquitoes**. Chapman, H.C., A.R. Barr, M. Laird, and D.E. Weidhaas, Eds., American Mosquito Control Association Bull. 6, pp. 3-17.
- Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecol. Monog.* 65: 21-74.
- Merritt, R.W., and K.W. Cummins. 1984. **An Introduction to the Aquatic Insects of North America, 2nd Ed.** Kendall/Hunt Publishing Co., Dubuque, IA.
- Middleton, M.J., J.D. Bell, J.J. Burchmore, D.A. Pollard and B.C. Pease. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales (Australia). *Aquat. Bot.* 18: 89-110.
- Miller, C.A. 1959. The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Apanteles fumiferanae* Vier. *Can. Entomol.* 91: 457-77.
- Milne, B.T. 1988. Measuring the fractal geometry of landscapes. *Appl. Math. Comput.* 27: 67-79.
- Minello, T.J., and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: The effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Bio. Ecol.* 72: 211-231.
- Minnaert, M. 1954. **The Nature of Light and Colour in the Open Air**. Dover Publications Inc., New York, NY.
- Mitchell, R. 1977. Bruchid beetles and seed packaging by palo verde. *Ecology* 58: 644-51.
- Mittelbach, G.G. 1981a. Foraging efficiency and body size: a study of optimal diet and habitat use by Bluegills. *Ecology* 62: 1370-1386.

- Mittelbach, G.G. 1981b. Patterns of invertebrate size and abundance in aquatic habitats. *Can. J. Fish. Aquat. Sci.* 38: 896-904.
- Mittelbach, G.G. 1983. Optimal foraging and growth in bluegills. *Oecologia* 59: 157-162.
- Monteith, L.G. 1955. Host preferences of *Drino bohemica* Mesn. (Diptera: Tachinidae), with particular reference to olfactory responses. *Can. Entomol.* 87: 509-30.
- Moran, M.D., and L.E. Hurd. 1994. Short-term responses to elevated predator densities: Noncompetitive intraguild interactions and behavior. *Oecologia* 98: 269-273.
- Moran, M.D., T.P. Rooney, and L.E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. *Ecology* 77: 2219-2227.
- Morse, D.H., J.H. Lawton, M.M. Dodson, and M.H. Williamson. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314: 731-733.
- Morse, D.H., N.E. Stork and J.H. Lawton. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecol. Entomol.* 13: 25-37.
- Mullin, S.J., R.J. Cooper and W.H.N. Gutzke. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). III. Searching for different prey types in structurally varied habitats. *Can. J. Zool.* 76: 548-555.
- Murakami, Y. 1983. Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). *Oecologia* 57: 72-77.
- Murdoch, W.W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.
- Murdoch, W.W., S. Avery, and M.E.B. Smyth. 1975. Switching in predatory fish. *Ecology* 56: 1054-1105.
- Murdoch, W.W., F.C. Evans and C.H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* 53: 819-829.
- Murdoch, W.W., R.F. Luck, S.L. Swarbrick, S. Walde, D.S. Yu, and J.D. Reeve. 1995. Regulation of an insect population under biological control. *Ecology* 76: 206-217.
- Murdoch, W.W., R.F. Luck, S.J. Walde, and D.S. Yu. 1989. A refuge for red scale under control by *Aphytis*: structural aspects. *Ecology* 70: 1707-1714.

- Murdoch, W.W., and A. Oaten. 1975. Predation and population stability. *Adv. Ecol. Res.* 9: 1-131.
- Need, J.T. and P.P. Burbutis. 1979. Searching efficiency of *Trichogramma nubilale*. *Environ. Entomol.* 8: 224-227.
- Nelson, W.G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *J. Exp. Mar. Biol. Ecol.* 39: 231-264.
- Nelson, W.G. 1980. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. *Bul. Mar. Sci.* 30: 80-89.
- Nentwig, W. 1982. Epigeic spiders, their potential prey and competitors: Relationship between size and frequency. *Oecologia* 55: 130-136.
- Norton, T.A., and M.R. Benson. 1983. Ecological interactions between the brown seaweed *Sargassum muticum* and its associated fauna. *Mar. Biol.* 75: 169-177.
- O'Brien, W.J., N.A. Slade, and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57: 1304-1310.
- Ogden, J.C. and J.P. Ebersole. 1981. Scale and community structure of coral reef fishes: A long-term study of a large artificial reef. *Mar. Ecol. Prog. Ser.* 4: 97-104.
- O'Neil, R.J. and J.L. Stimac. 1988a. Measurement and analysis of arthropod predation on velvetbean caterpillar, *Anticarsia gemmatilis* (Lepidoptera: Noctuidae), in soybeans. *Environ. Entomol.* 17: 821-826.
- O'Neil, R.J., and J.L. Stimac. 1988b. Model of arthropod predation on velvetbean caterpillar (Lepidoptera: Noctuidae) larvae in soybeans. *Environ. Entomol.* 17: 983-987.
- Orr, B.K., and V.H. Resh. 1989. Experimental test of the influence of aquatic macrophyte cover on the survival of *Anopheles* larvae. *J. Amer. Mosq. Contr. Assoc.* 5: 579-585.
- Orr, B.K., and V.H. Resh. 1991. Interactions among aquatic vegetation, predators and mosquitoes: Implications for management of *Anopheles* mosquitoes in a freshwater marsh. *Proc. Pap. Annu. Conf. Calif. Mosq. Vector Control Assoc.* 58th, pp. 214-220.
- Orr, B.K., and V.H. Resh. 1992. Influence of *Myriophyllum aquaticum* cover on *Anopheles* mosquito abundance, oviposition, and larval microhabitat. *Oecologia* 90: 474-482.

- Osawa, A. 1995. Inverse relationship of crown fractal dimension to self-thinning exponent of tree populations: a hypothesis. *Can. J. For. Res.* 25: 1608-1617.
- Paine, R.T. 1966. Food web complexity and species diversity. *Amer. Natural.* 100: 65-75.
- Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *J. Fish. Res. Bd. Can.* 28: 1503-1510.
- Paulissen, M.A. 1987. Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. *Oecologia* 71: 439-446.
- Peitgen, H.-O., H. Jürgens, and D. Saupe. 1992. **Chaos and Fractals: New Frontiers of Science**. Springer-Verlag, New York, NY.
- Pennak, R.W. 1953. **Fresh-Water Invertebrates of the United States**. The Ronald Press Co., New York, NY.
- Pentland, A. 1986. Perceptual organization and the representation of natural form. *Artif. Intel.* 28: 293-331.
- Persson, L., J. Andersson, E. Wahlstrom, and P. Eklov. 1996. Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. *Ecology* 77: 900-911.
- Peters, R.H. 1983. **The Ecological Implications of Body Size**. Cambridge University Press, Cambridge, MA.
- Peters, R.H. and J.V. Raelson. 1984. Relations between individual size and mammalian population density. *Amer. Natural.* 124: 498-517.
- Peters, R.H. and K. Wassenberg. 1983. The effect of body size on animal abundance. *Oecologia* 60: 89-96.
- Peterson, C.H. 1982. Clam predation by whelks (*Busycon* sp.): Experimental tests of the importance of the prey size, prey density, and seagrass cover. *Marine Biol.* 66: 159-170.
- Pianka, E.R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47: 1055-1059.
- Pianka, E.R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4: 53-74.
- Pianka, E.R. 1978. **Evolutionary Ecology**. Harper and Row, New York, NY.

- Pimentel, D. 1961. An evaluation of insect resistance in broccoli, Brussels sprouts, cabbage, collards and kale. *J. Econ. Entomol.* 54: 156-58.
- Pimentel, D. 1965. Restoring the quality of our environment. In: President's Science advisory Committee 1965.- The White House, Washington, D.C.: 227291.
- Pielou, E.C. 1975. **Ecological Diversity.** John Wiley and Sons, New York, NY.
- Pontasch, K.W. 1988. Predation by *Paragnetina fumosa* (Banks) (Plecoptera: Perlidae) on mayflies: The influence of substrate complexity. *Amer. Midl. Natural.* 119: 441-443.
- Porter, B.A. 1928. The apple maggot. *U.S. Dep. Agric. Tech. Bull.* 66: 1-48.
- Poulson, T.L., and D.C. Culver. 1969. Diversity in terrestrial cave communities. *Ecology* 50: 153-157.
- Power, M.E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73: 733-746.
- Preston, F.W. 1948. The commonness and rarity of species. *Ecology* 29: 254-283.
- Price, M.V. 1983. Ecological consequences of body size: A model for patch choice in desert rodents. *Oecologia* 59: 384-392.
- Price, P.W., C.E. Bouton, P. Gross, B.A. McPherson, J.N. Thompson and A.E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol. System.* 11: 41-65.
- Provencher, L., and S.E. Riechert. 1994. Model and field test of prey control effects by spider assemblages. *Environ. Entomol.* 23: 1-17.
- Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. *Quart. Rev. Biol.* 52: 137-154.
- Quade, H.W. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. *Ecology* 50: 170-179.
- Rabb, R.L. and J.R. Bradley. 1968. The influence of host plants on parasitism of eggs of the tobacco hornworm. *J. Econ. Entomol.* 61: 1249-52.
- Read, D.G. 1984. Movements and home ranges of three sympatric dasyurids, *Sminthopsis crassicaudata*, *Planigale gilesi* and *P. tenuirostris* (Marsupialia), in semiarid western New South Wales. *Austral. Wildlife Res.* 11: 223-234.

- Rejmankova, E., M. Remanek, M.J. Pitcairn, and R.K. Washino. 1987. Aquatic vegetation as a micro-habitat for rice field mosquitoes. *Mosq. Control Res. Ann. Rep.* 1987: 44-45.
- Richardson, L.F. 1961. The problem of contiguity: An appendix of statistics of deadly quarrels. *General Systems Yearbook* 6: 139-187.
- Ricklefs, R.E., D. Cochran and E.R. Pianka. 1981. A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology* 62: 1474-1483.
- Risk, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* No 153: 1-4.
- Ritz, K., and J. Crawford. 1990. Quantification of the fractal nature of colonies of *Trichoderma viride*. *Mycol. Res.* 94: 1138-1152.
- Robinson, J.V. and J.E. Dickerson Jr. 1987. Does invasion sequence affect community structure? *Ecology* 68:587-595.
- Robinson, J.V. and M.A. Edgemon. 1988. An experimental evaluation of the effect of invasion history on community structure. *Ecology* 69: 1410-1417.
- Rodriguez, J. and M.M. Mullin. 1986. Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol. Oceanogr.* 31: 361-370.
- Rodríguez, M.A. and W.M. Lewis Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecol. Monog.* 67: 109-128.
- Roland, J. and P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386: 710-713.
- Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: Habitat and environmental complexity. *Ecology* 50: 558-572.
- Rosine, W.N. 1955. The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. *Ecology* 36: 308-214.
- Rotenberry, J.T. 1985. The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia* 67: 213-217.
- Rotenberry, J.T. and J.A. Wiens. 1980. Habitat structure, patchiness and avian communities in North American steppe vegetation: A multivariate analysis. *Ecology* 61: 1228-1250.

- Roth, V.L. 1981. Constancy in the size ratios of sympatric species. *Amer. Natural.* 118: 394-404.
- Rundle, S.D. and S.J. Ormerod. 1991. The influence of chemistry and habitat features on the microcrustacea of some upland Welsh streams. *Freshwat. Biol.* 26: 439-452.
- Russ, G.R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *J. Exp. Mar. Biol. Ecol.* 42: 55-69.
- Russell, E.P. 1989. Enemies hypothesis: A review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entomol.* 18: 590-599.
- Russo, A.R. 1987. Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. *Mar. Ecol. Progr. Ser.* 36: 101-105.
- Ryer, C.H. 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Mar. Ecol. Progr. Ser.* 48: 37-45.
- Savino, J.F. and R.A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Amer. Fish. Soc.* 11: 255-266.
- Savino, J.F. and R.A. Stein. 1989. Behavioural interactions between fish predators and their prey: Effects of plant density. *Anim. Behav.* 37: 311-321.
- Savino, J.F., E.A. Marschall, and R.A. Stein. 1992. Bluegill growth as modified by plant-density: An exploration of underlying mechanisms. *Oecologia* 89: 153-160.
- Scheffer, M., A.A. Achterberg, and B. Beltman. 1984. Distribution of macro-invertebrates in a ditch in relation to the vegetation. *Freshwat. Biol.* 14: 367-370.
- Schmitt, R.J., and J.A. Coyer. 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): Importance of foraging behavior in prey size selection. *Oecologia* 55: 369-378.
- Schoener, T.W. 1965. Evolution of bill size differences among congeneric species of birds. *Evolution* 19: 189-213.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology* 49: 704-726.
- Schoener, T.W., and D.H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size pattern. *Amer. Natural.* 102: 207-224.

- Schroeder, M. 1991. **Fractals, Chaos, Power Laws: Minutes from an Infinite Paradise.** W.H. Freeman and Co., New York, NY.
- Schwinghamer, P. 1981. Characteristic size-distributions of integral benthic communities. *Can. J. Fish Aquat. Sci.* 38: 1255-1263.
- Schwinghamer, P. 1985. Observations on size structure and pelagic coupling of some shelf and abyssal benthic communities. In: *Proceedings of the 19th European Marine biology Symposium*, ed. P.E. Gibbs, Cambridge University Press, Cambridge, U.K. pp. 347-359.
- Shannon, C.E., and W. Weiner. 1963. **The Mathematical Theory of Communication.** University of Illinois Press, Urbana, IL.
- Shorrocks, B., J. Marsters, I. Ward, and P.J. Evennett. 1991. The fractal dimension of lichens and the distribution of arthropod body lengths. *Funct. Ecol.* 5: 457-460.
- Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and body size relationships. *Nature* 380: 704-706.
- Simberloff, D. 1984. Properties of coexisting bird species in two archipelagoes. pp. 234-253. *In.. Ecological Communities: Conceptual Issues and the Evidence.* Strong, D.R., D. Simberloff, L.G. Abele, and A.B. Thistle, Eds., Princeton University Press, Princeton, NJ.
- Simberloff, D., and W. Boecklen. 1981. Santa Rosalia reconsidered: size ratios and competition. *Evolution* 35: 1206-1228.
- Simpson, G.G. 1964. Species densities of North American recent mammals. *Syst. Zool.* 13: 57-73.
- Smith, C.L. and J.C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Bull. Nat. Hist. Mus. Los Angeles Co.* 14: 126-170.
- Smith, F.E. 1972. Spatial heterogeneity, stability, and diversity in ecosystems. *Trans. Conn. Acad. Art Sci.* 44: 307-336.
- Smith, L.D. and B.C. Coull. 1987. Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *J. Exp. Mar. Bio. Ecol.* 105: 123-136.
- Smith, R.L. 1980. **Ecology and Field Biology, 3rd Ed.** Harper and Row, New York, NY.
- Southwood, T.R.E. 1978. **Ecological Methods with Particular Reference to the Study of Insect Populations.** Chapman and Hall. London, UK.

- Sprules, W.G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology* 53: 375-386.
- Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58: 1237-1253.
- Stoner, A.W. 1979. Species specific predation on amphipod Crustacea by pinfish (*Lagodon rhomboides*): Mediation by macrophyte standing crop. *Marine Biol.* 55: 201-207.
- Stoner, A.W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Mar. Ecol. Prog. Ser.*, vol. 3: 537-551.
- Stoner, A.W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*. *J. Exper. Mar. Biol. Ecol.* 58: 271-284.
- Stoner, A.W., and F.G. Lewis, III. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *J. Exp. Mar. Biol.* 94: 19-40.
- Straalen, N.M., van. 1985. Size-specific mortality patterns in two species of forest floor Collembola. *Oecologia* 67: 220-223.
- Strayer, D. 1986. The size structure of a lacustrine zoobenthic community. *Oecologia* 69: 513-516.
- Streams, F.A. 1994. Effect of prey size on attack components of the functional response by *Notonecta undulata*. *Oecologia* 98: 57-63.
- Sugihara, G. 1980. Minimal community structure: An explanation of species abundance patterns. *Amer. Natural.* 116: 770-787.
- Talbot, F.H. 1965. A description of the coral structure of Tutia Reef (Tanganyika, East Africa) and its fish fauna. *Proc. Zoo. Soc. London* 145: 431-470.
- Tallamy, D.W., and R.F. Denno. 1979. Responses of sap-feeding insects (Homoptera-Hemiptera) to simplification of host plant structure. *Environ. Entomol.* 8: 1021-1028.
- Taylor, J.A., G.R. Friend and M.L. Dudzinski. 1984. Influence of sampling strategy on the relationships between fauna and vegetation structure, plant lifeform and floristics. *Austral. J. Ecol.* 9: 281-288.

- Taylor, R.A.J. 1988. A fractal approach to analysis of tree ring increments. Gen. Tech. Rep. SO-69. New Orleans, LA: USDA, Forest Service, Southern Forest Experiment Station: 40-56.
- Terakawa, N.I., and N. Ohsawa. 1981. On the arboreal arthropods in the Inabu experimental forest of Nagoya University. II. The relationship between body length and numbers of individuals. Japanese For. Disc. 91: 349-350.
- Thompson, D.J. 1975. Towards a predator-prey model incorporating age structure: The effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. J. Anim. Eco. 44: 907-916.
- Thorp, J.H. and E.A. Bergey. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology 62: 365-375.
- Thorp, J.H., and M.L. Cothran. 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. Ecology 65: 1546-1555.
- Tietze, N.S., and M.S. Mulla. 1989. Prey-size selection by *Triops longicaudatus* (Notostraca: Triopsidae) feeding on immature stages of *Culex quinquefasciatus*. J. Amer. Mosq. Control Assoc. 5: 392-396.
- Tolan, J.M., S.A. Holt and C.P. Onuf. 1997. Distribution and community structure of ichthyoplankton in Laguna Madre seagrass meadows: Potential impact of seagrass species change. Estuaries 20: 450-464.
- Tonkyn, D.W., and B.J. Cole. 1986. The statistical analysis of size ratios. Amer. Natural. 128: 66-81.
- Tostowaryk, W. 1972. The effect of prey defense on the functional response of *Podisus modestus* (Hemiptera: Pentatomidae) to densities of the sawflies *Neodiprion swainei* and *N. pratti banksianae* (Hymenoptera: Neodiprionidae). Can. Entomol. 104: 61-69.
- Turner, A.M. and G.G. Mittelbach. 1990. Predator avoidance and community structure: Interactions among piscivores, planktivores and plankton. Ecology 71: 2241-2254.
- Unger, P.A., and W.M. Lewis Jr. 1983. Selective predation with respect to body size in population of the fish *Xenomelaniris venezuelae* (Atherinidae) Venezuela. Ecology 64: 1136-1144.
- van Lenteren, J.C. 1980. Evaluation of control capabilities of natural enemies: Does art have to become science? Nether. J. Zool. 30: 369-391.

- Van Valen, L. 1973. Body size and numbers of plants and animals. *Evolution* 27: 27-35.
- Vanni, M.J., and D.L. Findlay. 1990. Trophic cascades and phytoplankton community structure. *Ecology* 71: 921-937.
- Vince, S., I. Valiela, N. Backus, and J.M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: Consequences for prey distribution and abundance. *J. Exp. Marine Biol. Ecol.* 23: 255-266.
- Vincent, B., H. Rioux and M. Harvey. 1991. Factors affecting the structure of epiphytic gastropod communities in the St. Lawrence River (Quebec, Canada). *Hydrobiologia* 220: 57-72.
- Virnstein, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199-2017.
- Walde, S.J., R.F. Luck, D.S. Yu, and W.W. Murdoch. 1989. A refuge for red scale: the role of size-selectivity by a parasitoid wasp. *Ecology* 70: 100-1706.
- Walter, D.E., and R.A. Norton. 1984. Body size distribution in sympatric oribatid mites (Acari: Sarcoptiformes) from California pine litter. *Pedobiologia* 27: 99-106.
- Walter, D.E., and D.J. O'Dowd. 1992. Leaf morphology and predators: effect of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). *Environ. Entomol.* 21: 478-484.
- Wangberg, J.K. 1977. A new *Tetrastichus* parasitizing tephritid gall-formers on *Chrysothamnus* in Idaho. *Pan-Pac. Entomol.* 53: 237-40.
- Ware, D.M. 1972a. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density and prey size. *J. Fish. Res. Board Can.* 29: 1193-1201.
- Ware, D.M. 1972b. Predation by rainbow trout: the influence of hunger, prey density and prey size. *J. Fish. Res. Board Can.* 30: 787-797.
- Warwick, R.M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Mar. Biol.* 92: 557-562.
- Washburn, J.D., and H.V. Cornell. 1979. Chalcid parasitoid attack on a gall wasp population (*Acraspis hirta* (Hymenoptera: Cynipidae)) on *Quercus prinus* (Fagaceae). *Can. Entomol.* 111: 391-400.

- Webb, D.G. and T.R. Parsons. 1991. Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods: Field experiments in a subtidal seagrass bed. *Mar. Biol.* 109: 4485-492.
- Webster, J.A. 1975. Association of plant hairs and insect resistance: an annotated bibliography. U.S. Dep. Agric. Misc. Publ. 1297: 1-18.
- Werner, E.E., and D.J. Hall. 1974. Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042-1052.
- Werner, E.E., and G.G. Mittelbach. 1981. Optimal foraging: Field tests of diet choice and habitat switching. *Amer. Zool.* 21: 813-829.
- Weseloh, R.M. 1976. Behavior of forest insect parasitoids. In: **Perspectives in Forest Entomology**. Anderson, J.F., and H.K. Kaya, Eds., Academic Press, New York, NY. Pp. 99-110.
- Whiteside, M.C. and R.V. Harmsworth. 1967. Species diversity in chydorid (Cladocera) communities. *Ecology* 48: 664-667.
- Whittaker, R.H. 1975. **Communities and Ecosystems**. MacMillan Publishing Co., New York, NY.
- Wickham, J.D., and D.J. Norton. 1994. Mapping and analyzing landscape patterns. *Landscape Ecol.* 9: 7-23.
- Wiedenmann, R.N., and R.J. O'Neil. 1991. Laboratory measurement of the functional response of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Environ. Entomol.* 20: 610-614.
- Wiens, J.A. 1982. On size ratios and sequences in ecological communities: are there no rules? *Ann. Zool. Fenn.* 19: 297-308.
- Williams, C.B. 1953. The relative abundance of different species in a wild population. *J. Anim. Ecol.* 22: 14-31.
- Wilson, D.S. 1975. The adequacy of body size as a niche difference. *Amer. Natural.* 109: 769-784.
- Winemiller, K.O., and E.R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecolog. Monogr.* 60: 27-55.
- With, K.A. and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446-2459.

- Woets, J., and J.C. van Lenteren. 1976. The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporarum* (Homoptera: Aleyrodidae). VI. The influence of the host plant on the greenhouse whitefly and its parasite *Encarsia formosa*. Proc. 3rd Conf. Biol. Control Glasshouses O.I.L.B./S.R.O.P. 76: 125-37.
- Wolheim, W.M., and J.R. Lovvorn. 1996. Effects of macrophyte growth forms on invertebrate communities in saline lakes of the Wyoming High Plains. *Hydrobiologia* 323: 83-96.
- Woodin, S.A. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. *Ecology* 59: 274-284.
- Woodin, S.A. 1981. Disturbance and community structure in a shallow water sand flat. *Ecology* 62: 1052-1066.
- Worthen, W.B. 1989. Predator-mediated coexistence in laboratory communities of mycophagous *Drosophila* (Diptera: Drosophilidae). *Ecol. Entomol.* 14: 117-126.
- Worthen, W.B., M.L. Carswell, and K.A. Kelly. 1996. Nested subset structure of larval mycophagous fly assemblages: Nestedness in a non-island system. *Oecologia* 107: 257-264.
- Young, D.K., and M.W. Young. 1978. Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River estuary, Florida. *J. Marine Res.* 36: 569-593.
- Zaret, T.M. 1980. **Predation and freshwater communities.** Yale University Press, New Haven, CT.
- Zaret, T.M., and W.C. Kerfoot. 1975. Fish predation on *Bosmina longirostris*: body-size selection versus visibility selection. *Ecology* 56: 232-237.
- Zeide, B., and C.A. Gresham. 1991. Fractal dimensions of tree crowns in three loblolly pine plantations of coastal South Carolina. *Can. J. For. Res.* 21: 1208-1212

BIOGRAPHICAL SKETCH

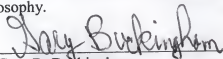
Robert Glen Lowen was born 01 June 1962, in Winnipeg, Manitoba, Canada. He attended the University of Manitoba where he obtained a Bachelor of Science/Ecology degree in 1985 and a Master of Science/Entomology degree in 1989. He worked for a few years for the Government of Canada, Department of Fisheries and Oceans, at the Freshwater Institute in Winnipeg. He came to The University of Florida to pursue a doctorate in the fall of 1992 and worked on several projects including taxonomy and biological control before settling on theoretical ecology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



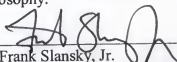
Dale H. Habeck, Chair
Professor of Entomology and
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Gary R. Buckingham
Assistant Professor of Entomology and
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Frank Slansky, Jr.
Professor of Entomology and
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Benjamin M. Bolker
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

William E. Peters
Professor of Entomology and
Nematology

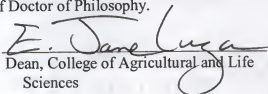
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Charles E. Cichra
Associate Professor of Fisheries and
Aquatic Sciences

This dissertation was submitted to the Graduate Faculty of the College of Agricultural and Life Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 2001


Dean, College of Agricultural and Life
Sciences

Dean, Graduate School

LD
1780
2001

.L917

UNIVERSITY OF FLORIDA



3 1262 08555 3609